USE OF SOUND FOR FISH PROTECTION AT POWER PRODUCTION FACILITIES: A HISTORICAL PERSPECTIVE OF THE STATE OF THE ART

Assessment of Technologies to Improve Measurement Capabilities in the Columbia River Fish and Wildlife Program

Phase I Final Report
Evaluation of the Use of Sound to Modify the Behavior of Fish

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Executive Summary

The search for effective and economical ways to modify fish behavior without physical intervention is one of the greatest challenges in fish management, particularly relative to electric power production. Physical barriers pose health risks to fish, reduce available water flow, and incur high maintenance costs. The challenge, then, is to find non-physical alternatives for fish behavior modification, and the use of sound holds promise as a fish protection device at power-production and water-control facilities. This paper is a studied response to this challenge by (1) summarizing the current state of the knowledge of how and what fish hear and (2) providing a starting place for investigation into the use of sonic behavior modification at power-production facilities of the Columbia River Basin, particularly within the context of recovery and maintenance of anadromous and resident fish stocks.

This paper summarizes the physics of sound in water, the physiology of fish hearing systems, and the behavioral responses of fish to sound. From the vast literature of hydrodynamics and fish hearing, this paper has extracted those aspects that hold the most promise in identifying elements critical to the success or failure of sounddeterrence system development at power-production facilities. The unique sound-propagation conditions in water have profoundly influenced the evolved differentiation of fish hearing systems from those of terrestrial animals. Fish have highly sophisticated sound-sensory systems, known as the octavolateralis system, by which they detect, extract, and process information from both hydrodynamic and acoustic components of sound fields. The-fish's primary hydrodynamic and acoustic sensor (or transducer) is the hair cells contained in the lateral-line sensory organs. Neural discharges from the fish's lateral-line neuromasts respond to water temperature, stimulus frequency, and directional orientation. There is also indirect stimulation, i.e., transduction of acoustic pressure to water-particle motion, via swim bladders and other structures. In addition to the mechanoreceptivity of the lateral line, the otolith organs of the inner ear are directly and indirectly stimulated by sound. Whereas the lateral line functions best within the zone nearest the sound source, the inner ear performs best in the far edges of the near field and outward.

There is a broad between-species range of hearing capabilities among fishes, e.g., fish with Weberian ossicles or prootic auditory bullae are considered "hearing specialists," whereas the salmonids, lacking such adaptations, respond only to particle motion and not acoustic pressure. It appears that those fish with functioning pressure-to-motion transducers have a very definite advantage in all areas of hearing, including localization of sound sources. Mechanisms of sound localization are not completely resolved, especially in the far field. The lateral line's varying morphologies apparently enable it to attenuate or amplify certain sound frequencies, and many species can discriminate among frequencies and detect tones masked by noise. Temporal characteristics of sound are also important in the fish's detection and response as well as in our development of fish behavior-modification systems; however, there is considerable between-species variation. Generally speaking, short-duration sounds must be louder, and crescendo wave forms significantly raise response thresholds. Fish have varying sensitivities to background noise, e.g., cod are especially sensitive whereas salmonids, with a generally lower sensitivity to sound, are less limited by background noise. Also, fish display varying abilities to overcome the masking effect of background noise in the far field and, through spatial filtering, to discriminate against noise. Consideration of these species-dependent characteristics is important in

eliciting spontaneous-avoidance reactions in fish. It is also important to recognize that functioning of the octavolateralis system can be disabled by high-intensity sound (such as explosives) and gas-bubble disease.

Drawing on the extensive literature base, a historical review of both physiological investigations and biological-engineering efforts pertaining to hearing in fish is presented. Whereas physiological investigations have expanded the knowledge base about mechanisms of fish hearing, biological engineering efforts have been problemoriented, e.g., using sound to evoke avoidance responses in migrating salmonids that prevent their entrainment in turbine flows. Important pioneering efforts in biological engineering include the sound-barrier studies of VanDerwaJker and EPRI's advanced intake technologies studies. Newer approaches to biological engineering are presented in a case study of the Army Corps of Engineers' sound-deterrence system at the Richard B. Russell hydropower project on the Savannah River in Georgia and of the New York Power Authority's sounddeterrence system at the James A. Fitzpatrick nuclear generating station on Lake Ontario. The physiological approach is demonstrated by a case study of Norwegian research that succeeded in clarifying the physiological basis of salmonid sound deterrence. The lessons learned from both physiological and biological-engineering approaches are summarized relative to salmonid responses to sound and the effectiveness of fish-protection systems at power-production facilities. The-se lessons indicate that sound deterrence for salmonids is possible only at short ranges using very low frequencies, carrying with it both positive and negative implications for the fish as well as the hydromechanics of generating the appropriate sound fields. Factors of sound-field avoidance, such as differential behavior of smolt vs.hatchery salmonids and among varying age groups, are discussed.

The advances described throughout this paper provide the foundation for further understanding of hearing mechanisms in fish and for further development of sonic behavior-modification systems. The remaining significant challenges relative to the Columbia River Basin Fish and Wildlife Program are considered, including (1) the feasibility of sounddeterrence systems for particular species and sites, (2) the necessity of defining a specific application and response in developing sound-deterrence systems, (3) the importance of bilateral utilization of state-of-the-art physiological and biological-engineering approaches, (4) clearly determining the adequate sound stimulus for salmonid avoidance response, (5) acknowledging the lack of important information, pertaining to Columbia River Basin species and their acoustic environment, which must be addressed if feasibility of sound-deterrence systems is to be adequately evaluated, (6) the unavoidable complications and ambiguity surrounding the multiplex factors of salmonid response to sound stimuli, including species, age, physiological state, prior conditioning, and environmental variables, and (7) the realization that sound-sensory systems of fish can be disabled by gas bubble disease.

Introduction

This paper summarizes the current state of the knowledge of fish hearing, i.e., what is known about fish response to sound, and provides a starting place for investigation into the use of sonic behavior modification to help solve pressing problems in the maintenance and recovery of anadromous and resident fish stocks of the Columbia River Basin. The challenge for scientists and engineers is to understand 1) how and what fish hear, and 2) how to use this knowledge to influence fish behavior or to factor fish sensory systems and behavior into the design of fish protection devices at power-production and water-control facilities. The sections that follow are a studied response to this challenge.

In many respects, the search for effective and economical ways to modify fish behavior without physical intervention is one of the grails of fish management, particularly (although not exclusively), relative to electric power production. Within the Columbia River Basin and elsewhere, water is put to many uses not conducive to the health of indigenous fish. Irrigation, impoundment, and hydropower production frequently modify the riverine environment to the detriment of indigenous stocks while creating productive environments for competing or predatory species. The mechanisms of impact are numerous. Water project managers, when faced with the need to reduce impacts of their operations on fish health, generally attempt to divert fish from high-risk to lower-risk regions or manage the environment in such a way as to increase the survival prospects of impacted species. Almost without exception, risk reduction is accomplished by using physical barriers of one form or another. Untbrtunately, physical barriers at water projects have several drawbacks, e.g., reducing available water flow for energy production and incurring high maintenance costs. In addition, recent studies (Sale et al. 1991) have documented that once these barriers are installed, they are rarely evaluated for effectiveness relative to design goals and/or regulatory mandates, and even less rarely monitored throughout the life of their use. All in ah, there is interest-if not enthusiasm-across the spectrum, from project owners to regulators, in finding alternatives to physical barriers such that risks to fish health can be reduced during their encounter with water-control facilities.

Sonic behavior modification holds promise in positively influencing fish behavior at power-production or water-control projects. After ah, it is common knowledge that fish "hear" and react to what they hear, and the use of sound to influence fish behavior is an old idea. Sports fishermen pay extra for "sonic" lures and are unabashed in their discussions of the effectiveness of favorite sound-emitting lures. Fishing lore includes lessons on stealthy approaches to favorite streamside fishing spots and the necessity of remaining quiet in the boat or else risk poor catches. Commercial fishermen, knowing that fish avoid boats and nets, spend much time and money attempting to become more stealthy and outsmart the ability of fish to avoid nets. The examples would fill a book.

For physical reasons, sound is ubiquitous underwater. Sound-propagation conditions are much better underwater than in air. Sound travels farther and faster in water, and with less loss, than in air. Also, sound is reciprocal: if you can hear, you are also being heard. For these reasons, detection and analysis of sound, and reaction to it, are "life and death" issues for fish. Fish have developed highly sophisticated sound sensory systems which differ markedly from those of terrestrial animals and humans.

For humans, sound is the means of choice for many underwater tasks, including communications and remote sensing. While the velocity of sound in water ($\sim$ 1500 m/set) is slow compared with the velocity of electromagnetic radiation in air ($\sim$ 300 million m/set), sound is more useful because it attenuates with distance at a much lower rate. For example, at 500 hertz (Hz) sound is attenuated (considering absorption, the more frequency-dependent component of transmission loss) 1 decibel or dB (-20%) in 100 km of saltwater or in 10,000 km of freshwater. In contrast, electromagnetic radiation at 500 Hz attenuates 1 dB in 1 meter of air.

The primary function of the hearing system in fish is to allow them to form a three-dimensional perspective of their environment. Sound conveys information fish use to sense their surroundings, locate food, avoid predation, and perform a variety of other tasks. The many thousands of fish species, over 500 million years of evolution, have developed a very wide range of capabilities for using information in sound fields to their benefit. Although extrapolating the human hearing experience to fish may be intellectually and emotionally appealing, it is not particularly useful in understanding the fish hearing system, known to scientists as the octavolateralis system. In a physiological context, the octavolateralis system includes the inner ear and the lateral-line sensory systems, the organs of which are innervated by the eighth and lateral-line cranial nerves.

Gaining a better understanding of the octavolateralis system takes us only partway toward a better understanding of hearing in fish, the other necessary understanding being the physics of sound in water. Sound propagation in water differs quite significantly from sound propagation in air, and these differences have, of course, profoundly influenced the evolved differentiation of fish hearing systems from those of terrestrial animals including humans. There is a wealth of information available on the physics of sound in water, the physiology of fish hearing systems, and the behavioral responses of fish to sound. For this paper, I have extracted from the literature those aspects of the octavolateralis system and the physics of sound in water that hold the most promise in identifying elements critical to the success or failure of sound-deterrence system development at power-production or water-control facilities.

Because of the history of failure, it has been easy to be very skeptical about the potential use of sound to influence fish behavior. However, recent experiences have shown that it is possible to use sound to influence fish behavior, to the benefit both of the fish and the power-production or water-control facilities. The record of success and failure of sonic behavior-modification systems is presented in the Findings and Discussion section. In addition to field-scale experiments into the use of sound, there has been considerable laboratory-scale work into the physiology and physics of fish hearing, much within the last decade. This body of work provides a wealth of valuable information on the responses of fish 'hearing" systems to components of a sound field.

Another potential application of sonic behavior modification is predation control for both migratory and resident fish. Predation is suspected in many cases, and has been shown in others, to be a major cause of mortality to migrating fish under natural conditions and potentially even more so where natural migratory patterns have been modified by humans. Among the possible benefits of a sound-deterrence system would be exclusion of predators by nonphysical means from the vicinity of fish bypass outfalls or at other vulnerable points in their migratory route, as well as using sound in other ways to reduce predator effectiveness.

Hydrodynamic Flow Detection and Hearing in Fish

Fish have sensors that detect and extract information from both hydrodynamic and acoustic components of sound fields. Information from these sensors is processed in a fish's central nervous system which gives fish truly impressive abilities to sense, interpret, and respond to their environment.

Physics of Sound in Water

It is no mystery why fish have evolved very sophisticated sound sensing systems. Compared with other energy forms that might be propagated underwater to carry information to fish sensory systems, sound has the lowest attenuation. At a frequency of 500 Hz, sound will attenuate only 1 dB, or 20%, over a range of 100 km in seawater and 10,000 km in freshwater. In contrast, under the moderately turbid conditions of many freshwater lakes and rivers, light attenuates to 1% or 20 dB relative to incident values within 10 m. One disadvantage of sound underwater is that water is a good conductor of sound. Any disturbance reaching the water from the surface, shore, machinery, etc., is propagated with little attenuation considerable distances from the source, making the underwater environment very noisy. The hearing of fish is most acute in that region (500 Hz $\pm$ 500 Hz) where ambient and manmade noise levels are highest (Urick 1967). This is also true of the underwater environment in the vicinity of hydropower plants (Anderson et al. 1989). The reason for sensitivity over this range is that many sources of life-and-death significance (such as the approach of a predator or prey, the warning tail flip of a startled neighbor, the vocalizations of conspecifics, and a host of other similar sources) create sound within this range.

Sound propagates through water, a compressible medium, in the form of longitudinal waves. Longitudinal means that the displacement of water particles is along the direction of propagation. However, this does not mean that sound propagates in a direct path from the source to the fish, except for certain classes of sources, for short ranges, and certain conditions related to location of the source near boundaries (surface, bottom, or structural) and the physical parameters (temperature and salinity) of the water. The complexity of the natural environment in these areas makes it difficult to scale-up from the laboratory to the field in order to apply knowledge of fish responses to sound stimuli.

The reader is referred to Appendix A for a more detailed introduction to hydrodynamics. Considerable literature is available on the physics of sound in water and the derivation and explanation of the relevant mathematics. Albers (1960) and Clay and Medwin (1977) are but two of a large number of good starting points into this literature. A comprehensive treatment of sound fields, their sources, and the stimuli of relevance to fish hydrodynamic and sound sensory systems is given by Kalmijn (1988).

Hair Cells: The Fish's Primary Sound Sensor

The basis of both hydrodynamic and acoustic sensors in fish is hair cells which respond to extremely small displacements of their ciliary bundles. All fish sensing of sound fields is mediated through hair cells; therefore, the necessary stimulus for hearing by fish is the movement of water particles. Because the oscillatory motions of water particles in sound fields are extremely small, the movement necessary to stimulate a hair cell is also very small. Water-particle displacements are measured in angstroms, a unit of measure with the dimensions of 10^{-10} m and the same unit used to measure distances such as the diameter of atoms. Hair cells are sensitive to mechanical deflections on the order of a thousandth of a degree, or about 0.35 angstroms (Hudspeth 1983, Kroese and van Netten 1989). Despite this high sensitivity, however, the rapid decrease in particle motion with distance in sound fields would result in fish being unable to detect sounds other than at very short distances from their source. Consequently, many species of fish have evolved structures to extend the range over which they can detect sound from its source, earning themselves the reputation of "hearing specialists." The structures that extend their ability to "hear" at longer distances will be discussed later. Regardless, it is important to remember the basic fact that if water particles are not moving, hair cells are not stimulated, and fish cannot hear.

Hair cells consist of a cell with a bundle of hairs on the upper surface. The hairs are systematically organized with a single larger kinocilium and a group of smaller-diameter and shorter stereocilia. The shortest kinocilium is on the order of $2\mu m$, the longest $20\mu m$ ($1\mu m = 10^{-6}m$). The stereocilia bundle is tapered away from the kinocilium (Figure 1). Clusters of hair cells, from a few 10s to more than 100 cells, are grouped into sensory units or organs. One type of sensory unit is the neuromast, typically found scattered over the head region of fish and coupled to the water by a gelatinous covering called a cupulae. Movement of water particles against the cupulae causes displacement of the cilia of hair cells in a neuromast. Displacement of hair-cell cilia toward the kinocilium causes nerve firing; displacements away from the kinocilium are inhibitory to nerve firing; and displacement in other directions follows a cosine-like response between excitation and inhibition. This directional-sensitive response makes the hair cells potential mechanisms for localization of underwater sound sources, determination of the direction of water currents, etc. (Hawkins 1986).

Clusters of hair cells within the lateral line, either as free neuromasts external to the lateral line or in the macula of the inner ear, form the basic sensory units of a fish's sound sensing system. Hair cells within a particular cluster are very uniform in morphology and orientation. Sensory clusters can vary in function, and these differences appear to be primarily determined by the peripheral structures that couple the hair cells to the environment. Such coupling can be direct to the water or indiect via some intermediate structure such as an otolith, i.e., a bony structure found in the fish inner ear (Dijkgraaf 1963, Roberts et al. 1988). Unlike most terrestrial animals with more neural fibers than hair cells, fish have more hair cells per fiber with a single neural fiber connecting to hair cells that may be quite far apart (Platt and Popper 1981).

The key point to remember about hair cells is that they are mechanical sensors. Hair cells do not respond directly to acoustic pressure; rather, physical displacement of hair-cell cilia is necessary for fish to hear. It is also important to keep in mind that hair cells are the basic mechanical-to-electrical transducer in the octavolateralis system and that, in almost all cases, the coupling of hair cells with the
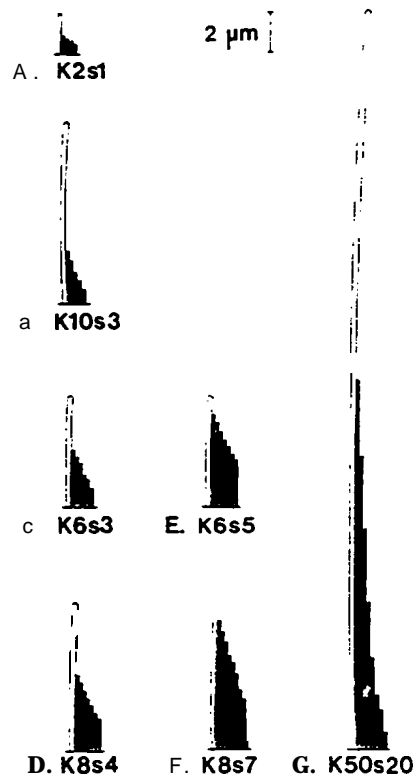
Figure 1. Schematic of the ciliary bundles from different inner ear endorgans of fish showing the wide range of lengths found in different regions. A to F are generally found on the otolith maculae; G is found only on the cristae of the simicircular canals. (From Platt & Popper 1981, p. 106, used with permission.)

sound-field stimulus is indirect through other structures. This indirect coupling means that at a sensor level, the sound-field stimuli that best correlates with octavolateralis sensor response are water-particle velocity and acceleration. (A sensor is the product of integration of a transducer with other components to enable deployment of the transducer in the environment and facilitate acquisition of the signals produced by the transducer.)

The Lateral Line

Mechanoreceptivity

The lateral-line system consists of a large number of sensory organs organized in linear arrays on the head and trunk of fish, these arrays ranging from simple to very complex (Figure 2). Extensions of the lateral line also occur as free organs frequently found in large numbers primarily in the head region of fish. The primary function of the lateral line is as a receiver of hydrodynamic and low-frequency
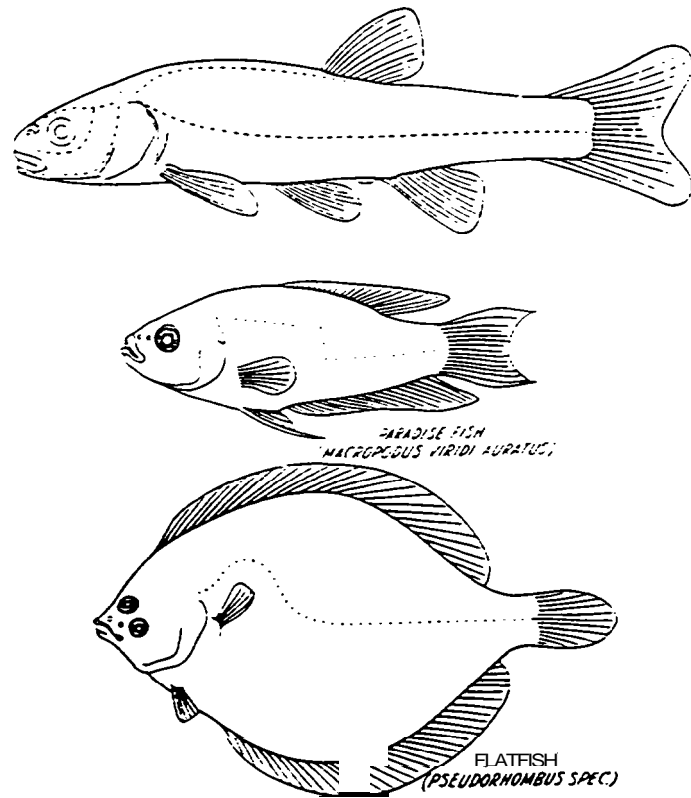
Figure 2. (top) Topogaphy of lateral lines in the minnow, phoxinus (from Coombs et al. 1989 (eds.), p. 9, used with permission); (middle and bottom) Dorsal displacement of anterior part of bunk lateral line which bypasses region of water disturbance cursed by movement of the pectoral fin (from Coombs et al. 1989 (eds), p. 10; used with permission).

water-particle motions that originate within a body length or two of the fish (Bleckmann 1993, Popper and Platt 1993, Kalmijn 1989). The primary sensory element, or transducer, of all lateral-line organs is hair cells. Lateral-line sensory organs consist of clusters of hair cells coupled to the environment through a gelatinous covering called a cupulae. Deflections of the cupulae by water-particle movements cause bending of the hair cells, followed by the flow of ions across hair-cell membranes, resulting in electrical discharge by neurons.

There is considerable structural variation in the lateral lines of fish (Figure 3), ranging from cupulae in direct contact with the water, to membrane-enclosed cupulae in no direct contact with the outlying water (Denton and Gray 1983 and 1988, van Bergeijk and Alexander 1962, Harris and van Bergeijk 1962). These structural differences have led scientists to expect large differences in the mechanical properties of lateral lines and sensory specialization among fish (Popper and Fay 1993). There is also considerable between-species difference in the extent of the lateral-line system and the number and location of free neuromasts (Coombs et al. 1988).

Superficial Neuromasts

Narrow Canal Neuromasis

N'ce Canal Neuromasts

A   B

Figure 3. Schematic of the variation in the lateral line system of various fishes. (A) Side views of the cupula over neuromast of various forms, with water flow shown by arrows; in the narrow canal the press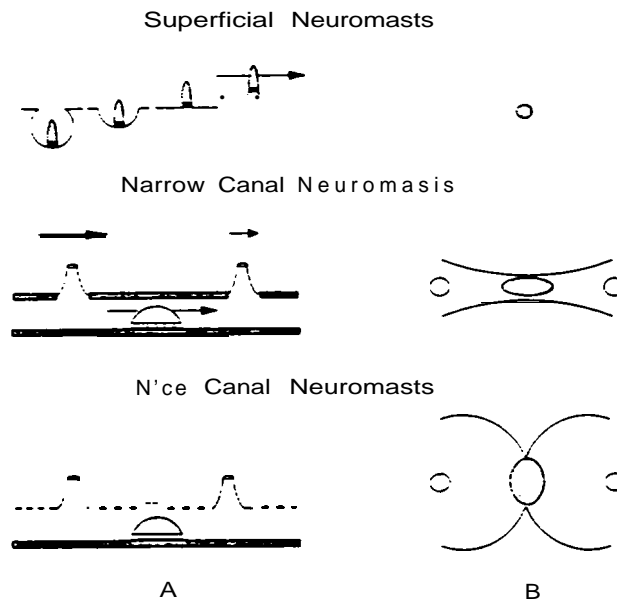ure flaw inside the canal is induced from water-pressure difference above the two pores. Heavy lines indicate firm structures; dashed lines indicate flexible soft tissue. (B) Top views looking directly down on the stippled cuphuae for the various forms shown in (A), and the canal shapes with the pores indicated as open circles. (From Popper and Platt 1993, p. 111; used with permission.)

Since the lateral line is a mechanoreceptive system, there must be a net difference between the motion of the fish and the surrounding water particles for sound and water currents to be detected. A sensory cluster within a lateral line is stimulated by movement of the cupula covering the hair-cell cilia relative to the wall of the lateral-line canal. Movement of the cupula results from movement of the fluid in the lateral-line canal or, in the case of cupulae in direct contact with the water, by viscous drag forces. Movement of the liquid results from a net pressure gradient along the section of canal containing the neuromast. The net pressure gradient is directly related to the net accelerations of water along the canal relative to the fish. Thus, at the systems level the lateral line detects the spatial derivative of the flow field (Demon and Gray 1988, Kalmijn 1988), whereas at the sensor level neural discharge is mediated by particle motion causing displacement of hair-cell cilia. If there is no net acceleration of water relative to the fish, the sensory cells are not stimulated. Such a situation would occur when a fish is carried passively along with the local flow or in a low-frequency sound field at greater distances from a sound source where the dimensions of the lateral line are small compared to the wavelength of sound.

Demon and Gray (1988) categorize the most likely stimuli for the lateral line into three groups: 1) Local pressure gradients caused by a fish's swimming movements; 2) mechanical disturbance caused by the fish's tissue as it moves, as in swimming; and 3) local pressure gradients originating external to

the fish such as the activities of neighboring fish, water impinging on objects such as rocks, and surface disturbances. Within group 3, components of the sound field generated by vibrating sources can also stimulate the lateral line.

The accumulation of evidence supports the role of the lateral line as a hydrodynamic receiver and as a detector of low-frequency sounds originating from sources within a few body lengths of the fish. The lateral line does not respond directly to the acoustic-pressure component of sound fields. In the case of vibrating sources, the lateral line is only directly stimulated at very short distances from the source where the generated acoustic field behaves like an incompressible flow. It is only at short distances from such sources that a net acceleration in local flow along the body of a fish is possible because of the rapid decrease in particle motion with distance. In general, the distance from the sound source within which the lateral line can be stimulated is considerably less than a wavelength within the frequency range of most fish, which extends from direct current (DC) to typically < 150 Hz (Kalmijn 1988). For many species this distance is less than 3 to 4 body lengths. While there can be considerable between-species difference in morphology of the lateral-line system, and consequently in function, the effective distance between a sound source and the fish's lateral line is short. For example, there are significant differences between the lateral-line systems of sprat and **Poromitra** and large differences in sensitivity. Studies by Demon and Gray (1988) indicate that Poromitra may be as much as 100 times more sensitive than sprat in the frequency range of 5-15 Hz.

The lateral line enables fish to very rapidly detect, localize, and react to near-sound sources. An example is that given by Stober (1969) of the immediate reaction by rainbow trout to a tail flip, the startle response of a neighbor. At distances near a source-a couple of body lengths-fluid motions generated by the source (e.g., tail flip) along the body of the fish-its lateral line-are sufficiently strong and contain enough information so that the fish can localize the source. This means that the lateral-line response can be fast and accurate but is restricted to short distances. At greater distances, because of the rapid degradation of the local flow component of the sound field, the differential in fluid motions along the fish decreases until the body of the fish is essentially in a uniform field; the result is that any stimulation of the lateral line would be overwhelmed by stimuli generated by the swimming motions of the fish itself.

Early experimentation (Hofer 1908) concluded that fish can "feel" at a distance through these sensory elements. An anthropomorphic analog for the function of the lateral line is extended touch, or feeling without direct physical contact. Experiments have determined that fish can sense and will respond to very weak water currents and that the lateral line enables detection of obstacles (Dijkgraaf 1963). Studies by Suckling and Suckling (1964) and Anderson and Enger (1968) suggest that water-particle movement of <0.5 m (0.5×10^{-6} m) stimulates nerve response. The threshold of cupulae displacement for nerve stimulation was estimated by Kuiper (1967) to be -25 angstroms (25×10^{-10} m). Schwartz (1974) showed that net water currents relative to fish motion as low as 0.025 mm/sec caused sufficient displacement for hair-cell nerve firing. More recent work suggests that the absolute sensitivity of hair cells to 140-Hz stimuli is manifest in deflections on the order of 1 nanometer (run) to -0.1 nm root mean square (10^{-6} to 10^{-9} m rms, or $2.83\,10^{-6}$ to $2.83\,10^{-9}$ m peak to peak). In the far field these deflections would correspond to acoustic pressures on the order of 102 **dB//μPa@1m** (Fay 1988).

Other investigation has shown that lateral-line segments on the head of surface-feeding fish enable them to detect and locate prey by locating the source of surface waves (Bleckmann 1993, Schwartz

1965 and 1971). Blind cave fish are known to be able to distinguish between complex shapes if permitted to swim close to objects (von Campenhausen et al. 1981, Weissert and von Campenhausen 1981). Other experiments have shown that blinded fish can sense the approach of objects or avoid obstacles (Dijkgraaf 1963). Apparently, fish can use the low-frequency sound generated by the motion of their body (in a method similar to that of echo location) to detect and identify, and perhaps even "image," objects in water (Walters and Liu 1967, Hassan 1988).

Escape or startle responses in fish are thought to be mediated by Mauthner cells. These cells are large, paired neurons that project from the medulla into contralateral body musculature. These cells obtain input from the octovolateralis system and other sensory systems. While Mauthner cells appear to mediate fish startle responses, how the directional component is obtained from sound fields by the octavolateralis system, transmitted to the Mauthner cells, and processed within the time frame of the response are not known (Fay 1988, Eaton 1984, Eaton and Nissanov 1985, Blaxter et al. 1981, Blaxter and Hoss 1981, Hackett and Faber 1983).

Responses to water temperature, stimulus frequency, and direction

Weber and Schiewe (1976) suggest that in the lateral line of steelhead trout, 1 to 26 lateral-line neuromasts are innervated by a single fiber. Neuromasts innervated by a single fiber are grouped as a sensory unit and, in salmonids, successive sensory units overlap. Consistent with findings for other species, they found that spontaneous neural discharges from sensory units increased linearly with temperature. Sensory unit discharges were also observed to vary with stimulus frequency. The response of the steelhead lateral line was found to be three to four discharges per cycle at frequencies of 1 to 10 Hz, usually two discharges per cycle at 10 to 40 Hz, and a single discharge per cycle at 40 to 110 Hz. At higher frequencies, the discharges of most sensory units no longer followed frequency although some maintained this capability up to 200 Hz. The upper limit of one-to-one tracking of frequency was observed to increase as water temperature increased Above 300 Hz, most sensory units were not responsive. Weber and Schiewe concluded that their studies agreed with those of other investigators in that the lateral line is responsive to stimuli of 1 to 345 Hz, with maximum sensitivity in the range of 10 to 170 Hz.

Weber and Schiewe (1976) also found a directional response in lateral-line sensory units. A single, afferent nerve fiber appears to innervate hair cells with maximum sensitivity in a specific direction. This follows from the observation that, in general, lateral-line hair cells seem to be oriented so that they are 180" out of phase. They found when monitoring a single nerve fiber that the sensory unit for that fiber **would** discharge only within the compression or rarefaction portion of the sound wave. Such highly directional sensory capability could be very important in detecting the approach of a predator or the movement of prey at the low frequencies (10 to 100 Hz) associated with such movements. Humans and most terrestrial animals are incapable of detecting specific phases of sound signals.

Indirect stimulation via transduction of acoustic pressure to particle motion

The distance range from a sound source within which the lateral line can be stimulated can be indirectly extended in fish species with swimbladders or other structures that function as transducers of

acoustic pressure to particle motion. The nature and functioning of the various pressure-to-motion transducers in fish will be discussed in more detail in the "Inner Ear" section. The function of the swimbladder in this role will be used as an example here.

The swimbladder undergoes volume changes in a pressure field because it is filled with a compressible medium, i.e., air. These volume changes generate a sound field that is very near the fish's lateral line, near enough to generate net accelerations of water along the fish's body of sufficient magnitude to stimulate the lateral-line neuromasts (Sand 1981). Higher sensitivity to sound was initially found in swimbladder-bearing fish (von Frisch 1938). Experimentation with these fish over the last few decades has shown their ability to detect both acoustic pressure and particle motion (Enger and Andersen 1967, Enger et al. 1973, Sand and Enger 1973, Chapman and Hawkins 1973, Sand 1974, Fay and Popper 1974 and 1975, Myrberg and Spires 1980, Buwalda 1981, Buwalda et al. 1983).

However, the presence of a swimbladder does not always mean markedly higher sensitivity. The location of the swimbladder and other aspects of its condition determine its utility as a pressure-to-motion transducer. In the case of salmonids, the location of the swimbladder and its general condition render it markedly ineffective as a pressure-to-motion transducer. Salmonids have been found to be more similar to non-swimbladder fishes than to species such as cod with swimbladders but without additional structures that aid in hearing. Indeed, it is the opinion of some investigators that the swimbladder has no function in the hearing of salmonids (Hawkins and Johnstone 1978).

Disability by high-intensity sound and disease

Functioning of the lateral line can be temporarily disabled by high-intensity sound. Weber and Schiewe (1976) found a 40 to 400 m/sec delay in the recovery of spontaneous neural activity in steelhead trout. The delay was a function of the frequency, amplitude, and duration of the sound stimulus. Such observations indicate that high-duty-cycle, high-intensity sound at frequencies above and beyond the optimum sensitivity band could effectively disable the lateral-line sensory system of steelhead and perhaps other salmonids. Because sensory cells in the inner ear have the same structure as those in the lateral line, they likely may show a similar response.

Functioning of the lateral line has also been shown to be severely disabled by gas bubble disease (Weber and Schiewe 1976). Steelhead trout exposed to water with a total gas pressure of 118% of saturation showed signs of gas bubble disease in the lateral line within 2 to 6 hrs. Progressive formation of bubbles within the lateral line resulted in progressive loss of function to the point of almost total unresponsiveness, Observation of fish following exposure showed recovery of sensitivity following resorption or dissipation of the bubbles in the lateral line. However, dissipation of bubbles within the lateral line required 16 to 20 hrs following return to equilibrated water. Given the many functions of the lateral line, including predatory avoidance, detection and avoidance of underwater objects, and orientation relative to water currents, the secondary sublethal effects of gas bubble disease (mediated by disabling the lateral line) could be quite detrimental to the survival of downstream migrants. Such decreased functioning could also negatively impact the effectiveness of sound behavioral barriers. The observations of the effect of gas bubble disease on the fish lateral line lead to questions about the potential for effects to the octavolateralis system by other diseases or exposures, such as the rapid pressure cycling experienced by fish passing through turbines.

The Inner Ear

Basic structure and function

The fish ear consists of a pair of internal structures symmetrically located on either side of a fish's head with no direct outlet to the exterior (Figure 4). Each ear consists of three semicircular canals with cristae and three otolith organs. Detailed descriptions can be found in several sources including Lowenstein (1971), Popper (1981, 1983), Platt and Popper (1981), Popper and Platt (1993) and Hawkins (1993). The various structures of the ear have four major functions: 1) maintenance and regulation of muscle tone; 2) detection of angular accelerations; 3) detection of gravity; and 4) detection of sound (Lowenstein 1971).

Direct stimulation via otolith organs

The otolith organs are the site of sound detection in the fish ear. Each otolitb organ consists of a bony otolith maintained by gelatinous membranes that mechanically couple the otolith to a sensory epithelium. The sensory epithelium contains hair cells with cilia that project toward the otolith. The hair cells are not attached to the otolith but indirectly coupled to it by the otolithic membranes. As in the case of the lateral line, mechanical bending of the cilia is the critical sensory stimulus for the organ. Sound cannot be detected unless it results in bending of sensory epithelium hair-cell cilia (Popper et al. 1992, Popper and Platt 1993).

Otoliths and their associated structures vary between species in size, orientation, and shape. Otoliths commonly have complex shapes with unique species-specific features that are believed to work in concert with the structure of the epithelium, accounting for between-species differences in hearing between species (Popper et al. 1992, Popper and Platt 1993). The epithelia of the inner ear show considerable variability and complexity in the number, orientation, and morphology of hair cells. Because of the presence of kinocilia, the orientation of hair cells is readily determined. Neighboring groups of hair cells frequently have different orientation whereas within-group orientation is quite uniform; as in the lateral line, this orientation has implications for directional hearing. There appears to be some standardization in the organization of hair-cell groups. A common pattern in one of the endorgans is that of four orientations in two pairs of hair-cell groups with opposing orientation (Popper and Platt 1993) (Figure 5).

In a sound field, the otolith organs move with different sound phases and amplitudes than the rest of the fish's body, which is approximately three times less dense with corresponding lesser inertia than the otoliths. The otoliths and hair cells in the sensory epitheiium are not directly linked. Rather, when stimulated by sound, the otoliths and sensory epithelium are displaced relative to each other. This relative displacement causes the cilia to bend and the hair cells to become stimulated. Bending of the cilia has been found to be proportional to acceleration of the otolith, and not to its displacement. In turn, otolith acceleration has been found to be proportional to the product of the square of the frequency of sound and acoustical displacement. Therefore, the response of the sensory elements is proportional to the product of acoustic pressure and frequency (Popper and Platt 1983, Saidel and Popper 1983, Rogers and Cox 1988).
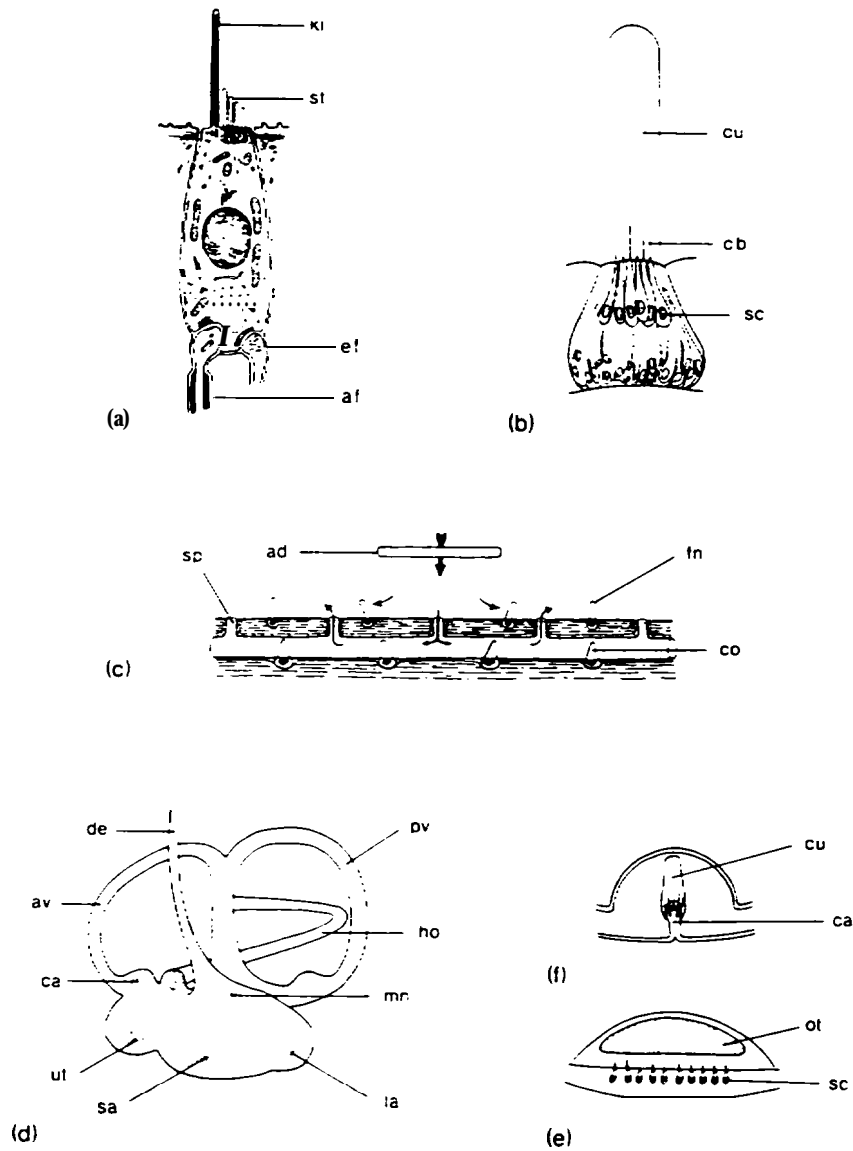
Figure 4. Lateral-line and inner-ear sense organs of fish. (a) Hair cell; ki=kinocilium, st=stereocilia, af=afferent nerve fiber, ef=efferent nerve fiber. (b) Lateral-line neuromast; sc=sensory cells, cb =ciliary bundles, cu =cupula, (c) Free neuromasts (fn) and lateral-line canal organs (co); sp=skin pores, ad=approaching disk. (d) Elasmobranch labyrinth; ut=utriculus, sa=sacculus, Ia=lagena, mn=macula neglecta, ca=crista ampullaris, ho=horizontal canal, av=anterior vertical canal, pv=posterior vertical canal, de=ductus endolymphaticus. (e) Utriculus; ot=otolithic mass, sc=sensory cells. (f) Apulla of semicircular canal; ca=crista ampullaris, cu=cupula. (From Kamijn 1988, p. 84, used with permission.)

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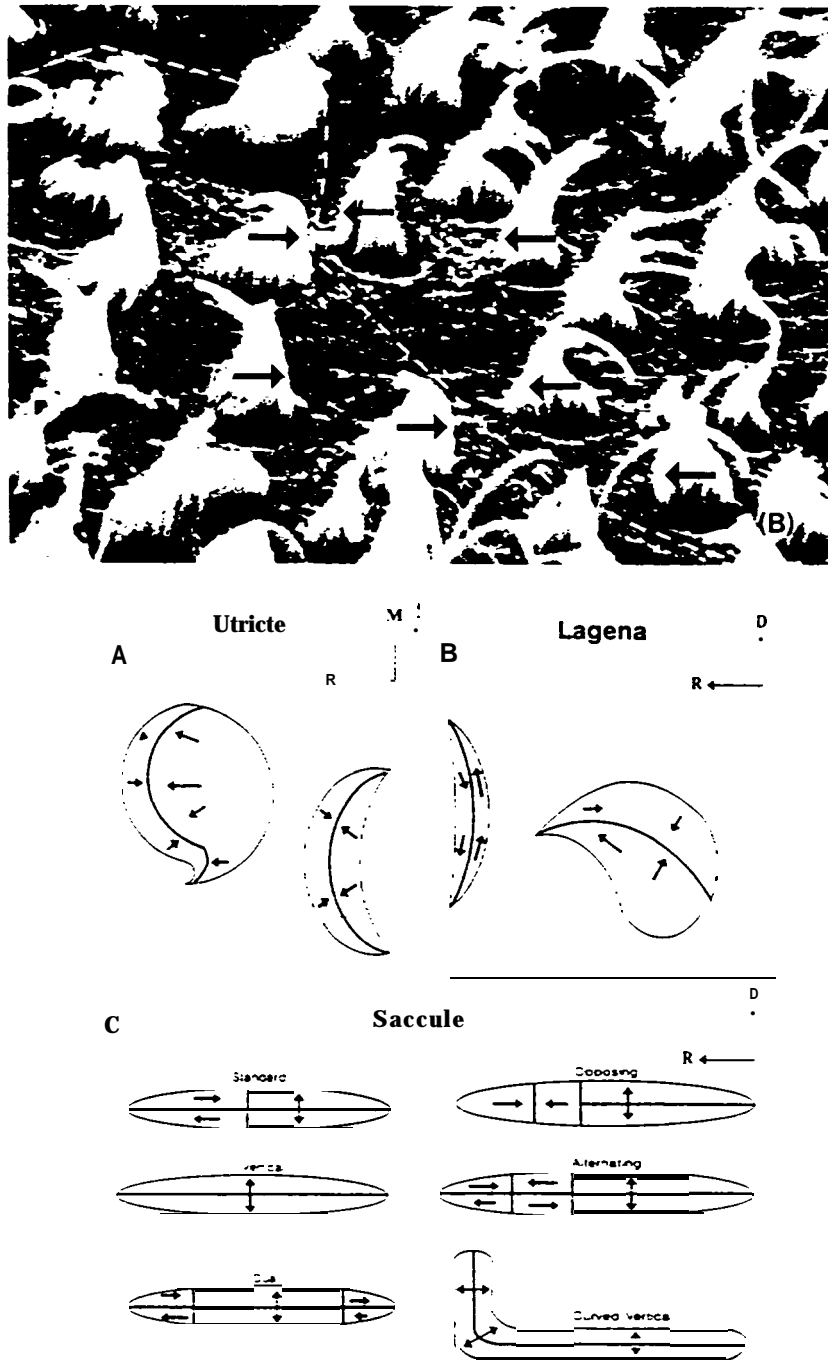
Figure 5. (top) Scanning electron micrograph of a field of hair cells from the lagenar epithelium of a zebrafish (*Brachydanio rerio*). Dashed dividing line separates two "groups" of hair cells oriented in opposite directions; arrows show directional orientation of each region. (From Popper and Platt 1993, p. 102; used with permission.) (bottom) Schematic of sensory hair-cell orientation patterns of otolithic endorgans in different fish species. Arrows indicate orientation of the bulk of hair cells in each "orientation group," based on ciliary bundle structure. (A) Two different utricular patterns; pattern on left is the most common among bony fish whereas pattern on right is found in a few species that may use their utricules for sound detection. (B) Lagenar epithelial pattern on the left is found in most teleosts whereas that on the right is found in otophysans. (C) Six different saccular patterns have been identified; D = dorsal, M = Medialateral, R = rostral. (From Popper and Platt 1993, p. 108; used with permission.)

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To understand hearing in fish, it is important to remember that the necessary stimulus for movement of the otoliths, and thereby stimulation of hair cells in the inner ear, is particle motion, and not acoustic pressure, as in the case of the lateral line. Detection of sound in the far field of sound sources where pressure predominates requires additional structures and some mechanism for transduction of pressure-to-particle motions of sufficient magnitude to stimulate the hair cells of the lateral line and/or inner ear.

Indirect stimulation via transduction of acoustic pressure to particle motion

Some fish species have both direct and indirect paths to the inner ear. In the direct path, the organs of the inner ear are stimulated by the particle-displacement components of sound independent of the swimbladder or other mediating structure. By the indirect path, fish can detect sound via acoustic pressure despite the fact that hair cells cannot respond to acoustic pressure. The indirect path requires a swim bladder or another special structure that acts as a pressure-to-motion transducer, as previously described for the indirect path to the lateral line. It should be noted, however, that the presence of a pressure-to-motion transducer does not necessarily mean that the species has enhanced hearing capability. An important example of this in the Columbia River Basin is the salmonids which, although possessing a swimbladder, have hearing similar to that of non-swimbladder-bearing species.

In the otophysans (catfishes, minnows, carps) who are considered "hearing specialists" because of their increased sensitivity to sound, the swimbladder is connected directly to otolith organs via a series of bones, the Weberian ossicles (Alexander 1962, van Bergeijk 1967). These bones physically connect the rostral end of the swimbladder to the fluid system of the inner ear (Figure 6). Fish with Weberian ossicles have been shown, in general but not without exception, to detect a wider range of frequencies and to have higher sensitivity than fish without these structures (Fay 1992, Schellart and Popper 1992, Popper and Platt 1993).

Other species considered "hearing specialists" have other special structures that function as pressure-to-motion transducers. In the clupeids (herrings, anchovies, alewives) the swimbladder, inner ear, and lateral line are all connected (Figure 7). The clupeids have a pair of prootic auditory bullae which act as pressure-to-motion transducers. The bullae, located in the head near the inner ear, are divided by a membrane into fluid- and gas-filled segments. The gas-filled segment is connected with the swimbladder, and the fluid-filled segment with the inner ear and head lateral line. Pressure changes cause the volume of gas in the bulla to change, causing liquid to flow in the inner ear and lateral line. These flows displace the hair cells of the various sensory units. In the clupeids the swimbladder acts as a reservoir to keep the volume of gas in the bullae constant when the fish changes depth. The swimbladder, in clupeids, does not appear important in maintenance of buoyancy (Allen et al. 1976, Blaxter et al. 1981).

Other significant adaptations of the swimbladder itself in other species include the Holocentridae (squirrelfishes), Percifbrmes (perches, snooks, basses), and Gadiformes (cods, hakes) wherein the swimbladder is attached to the skull adjacent to the inner ear. In the Mormyridae (elephantfishes) projections or bulbs on the end of the swimbladder enter the intracranial space (Platt and Popper 1981)
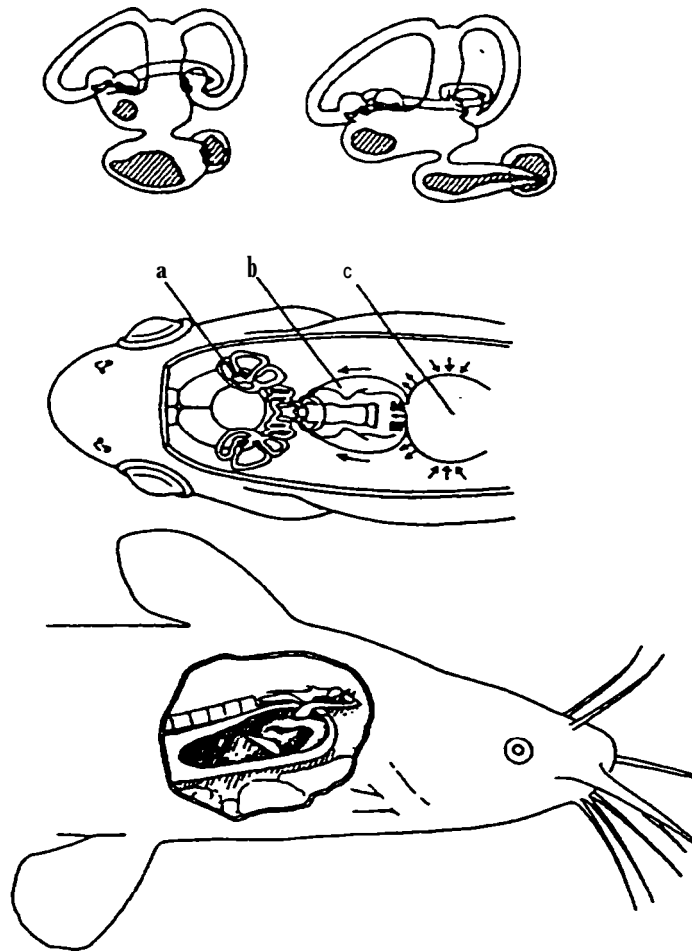
Figure 6. (top) Inner ears of fishes, like most vertebrate ears, possess three semicircular canals (equilibrium function) and an acoustic labyrinth with three sacs, each with a small dense chip of bony material within; example at left is of the inner ear of most fishes, while the inner ear of a cypriniform fish is shown at right. (middle) Cypriniform fishes have a special connecting link of bones that acoustically couple the swim bladder with fluids of the inner ear analogous to the mammalian middle ear bones. Swim bladder (c) serves as primary transducer in receiving sound, transmitting vibrations to the chair of four pairs of bones known as the Weberian apparatus (c) and then to the sacculus of the inner ear (a). (bottom) Side view of dissected catfish shows linkage from the swim bladder (opened) to first of the series of Weberian bones. (Redrawn from Tavolga 1965.)

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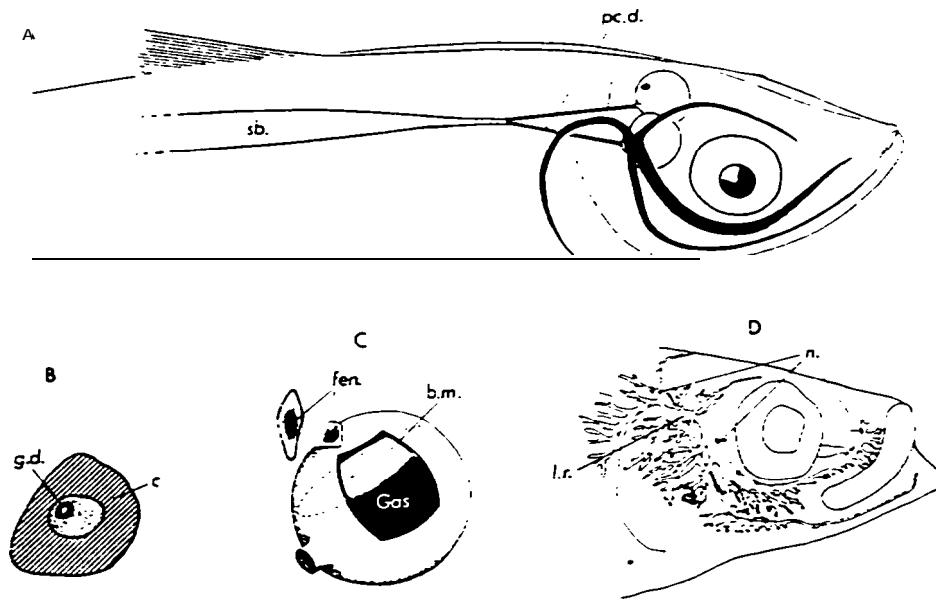
Figure 7. Special features of the clupeid acousticolateralis system are existence of the bullae (pressure-displacement converters), the hydrodynamical connections between the ear and lateral line, and the gas connections between the bullae and swimbladder which allow adaptation to depth. *(A)* **Position of two bullae, main lateral-line canals, and connections between bullae and swimbladder; sb = swimbladder, pc.d = precoelomic ducts. (B) Cross section of precoelomic duct between bulla and swimbladder; g.d. = small (about 7μm diameter) gas-filled central part; c = cartilage. (C) Bulla and its fenestta; b.m. = bulla membrane, fen=fenestra; elastic thread not shown. (D) lateral-line system of the sprat; l.r. = lateral recess, n=neuromasts. (From Tavolga et al. (eds.) 1981, p. 42; used with permission.)**

Hawkins and Johnstone (1978) concluded that the swimbladder in salmon plays no part in hearing. The swimbladder of salmonids is elongated and located well back from the skull, with no special structure or extensions to place it more directly in contact with the inner ear. This is in contrast to other swimbladder-bearing fish, such as cod which also lack Weberian ossicles or other special structures to assist hearing. In cod, the swimbladder is located nearer the skull and has a bulbous shape with the well-inflated end nearer the skull. Cod have been shown to detect sound pressure (Chapman and Hawkins 1973) whereas the salmonids have been shown to be sensitive primarily to particle motion. In terms of frequency response and sensitivity, salmonids are very like those species lacking a swimbladder. Other factors may also help explain this seeming anomaly. In addition to the location of the swimbladder, salmonids apparently do not keep their swimbladders as well inflated as do cod. Stressed salmonids often release gas, and observations of char indicate that the swimbladder frequently does not contain enough gas to make the fish neutrally buoyant (Sundnes and Bratland 1972). These factors would tend to significantly decrease the capacity of the salmonid swimbladder as a pressure-to-motion transducer, which helps explain their inability to use acoustic pressure to detect sound.

The primary, fundamental, and necessary stimulus for fish hearing is particle motion, whether by the direct or indirect path. Evidence indicates that the sound-displacement threshold can be very low. Regardless of this sensitivity, and because of the very rapid decrease in particle motion with distance from a sound source, hearing in fish without the indirect path would be limited to very short ranges, on
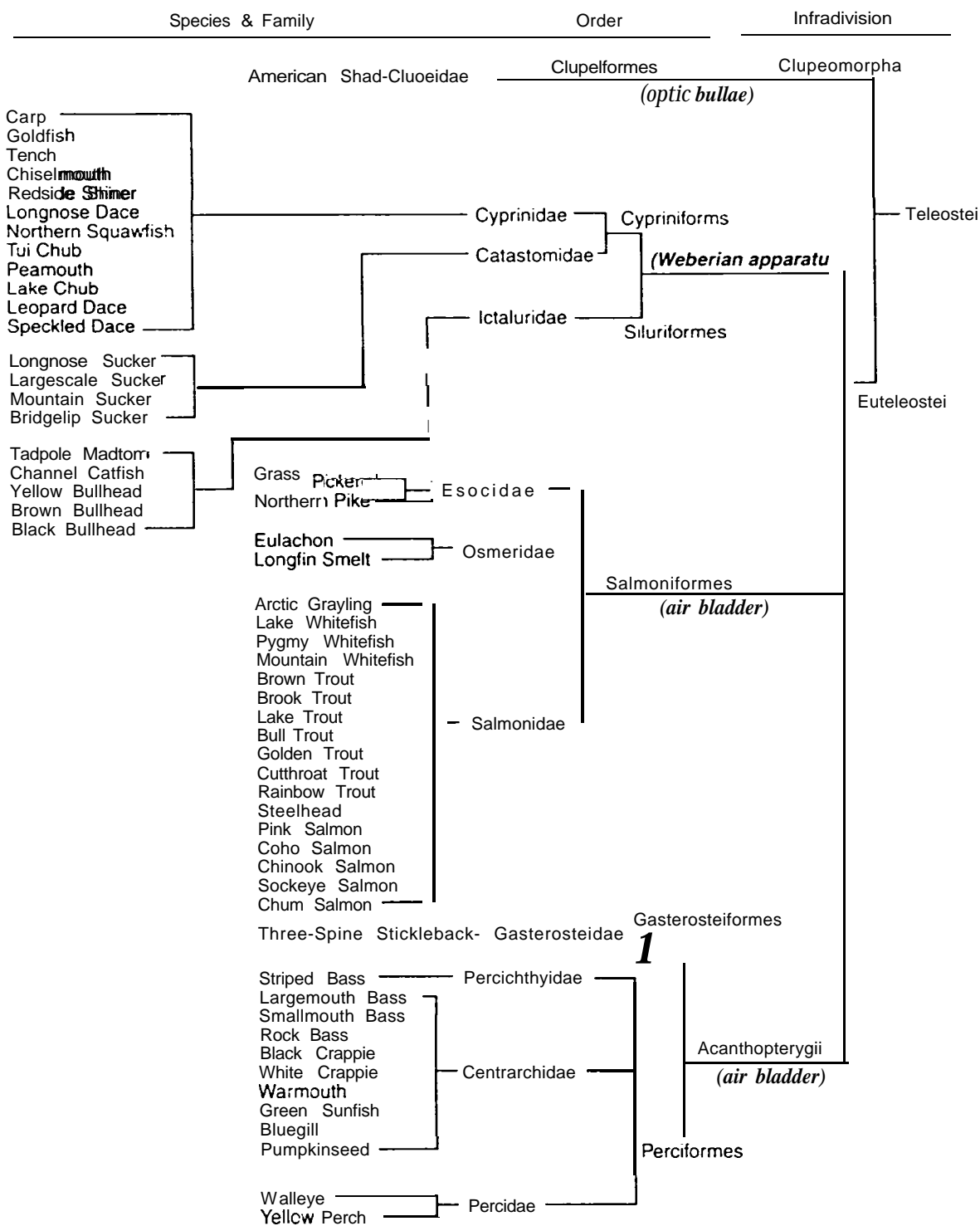
Figure 8. Fishes of the Columbia River Basin. (Modified from Nelson 1994, Wydoski and Whitney 1979.)

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the order of a fraction of a wavelength at infrasound frequencies or a few body lengths. With a pressure-to-motion transducer, the distance at which a fish can hear is dramatically extended. These structures also seem to extend frequency range and increase absolute sensitivity in most, but not all, of the species that have them.

Fishes present in the Columbia River Basin include representatives from groups with special adaptations, such as Weberian apparatus or prootic bullae, that make them "hearing specialists" as well as those lacking such adaptations, such as the salmonids. Figure 8 shows the fishes of the Columbia River Basin grouped according to these adaptations.

Damage by high-intensity sound

Some goldfish were killed and others suffered severe damage to their otolith organs following ¾-hour exposures to sound at 250 and 500 Hz at sound pressure levels of 182 to 204 **db//μPa@** 1 m (Hastings 1990). At 250 Hz, morphological damage to the otolith organs began at sound pressure levels of 189 **db//μPa@1m,** and at 500 Hz damage began at 197 **db//μPa@1m**. Scanning electron microscope inspection revealed that extended sound exposure destroyed the hair-cell cilia on the maculae of the saccular otolith organ. Hastings concluded that sound pressure levels at and above 180 **db//μPa@** lm are harmful to fish, whereas levels of 150 **dB//μPa@** lm and below will not harm fish. These tests also showed that the most susceptible species were those with extensions of the swimbladder in close proximity to the inner ear.

During operation of an acoustic fish-counting device in the mid-1980s at Stevens Dam, South Carolina, personnel of Bendix Corporation and South Carolina Wildlife and Marine Resources Division observed that blueback herring showed a strong avoidance response to 120 kHz sound at source levels of -200 **dB//μPa@1m)** (Al Menin, formerly of Bendix Corp., Sylmar CA, pers. commun.). They also observed that some blueback herring within – 6 feet of the sound source were **stunned** or killed. Accounting for the loss in sound pressure level that could have occurred in the 6 feet (< 6 **dB//μPa@** 1 m) between the transducer and the affected fish, it appears that the observed effects occurred at levels consistent with Hastings' (1990) findings.

It has been known for some time that explosives can kill or stun fish. Lethal thresholds for fish are between 229 and 234 **db//μPa@1m,** but sound can also cause significant sublethal damage to their octavolateralis system. One of the organs frequently found damaged in autopsies is the swimbladder. Fast rise-time explosives such as dynamite and TNT have lethal thresholds 5 to 10 dB lower than slow rise-time explosives. The thresholds for stunning by explosives are not known, nor the extent or nature of sublethal effects (MacLennan and Simmonds 1992). Although the sound levels and exposure periods required for damage are outside the current exposure range of fish behavior-modification systems, it appears prudent to be aware that the effects of sound on fish can be severe.

Mechanisms of Sound-Source Localization

The lateral line and inner ear perform sound-source localization differently. In addition, as a result of the way they are coupled to the water, the lateral line and ear perform best in different parts of

sound fields. For example, the lateral line functions best within the zone nearest the sound source where particle motion dominates sound fields. In contrast, the inner ear performs best in the far edges of the near field and, for fish with effective pressure-to-motion transducers, at considerably greater distances from the source.

The lateral line is concerned with frequencies < 200 Hz and with the very near field, sources that are within a few body lengths of the fish or that originate with the fish itself. The lateral line detects the net accelerations of the local flow field along the length of its sensory arrays which fall off as the fourth power of distance from the sound source. Larger fish with longer sensory arrays would appear to have a distinct advantage over a greater range in localizing a sound source. The local flow portion of the sound field generated by a source falls off very rapidly with distance so that different cupula along the lateral line will experience different deflections. Integration over these deflections provides information about the location of the sound source. This information integration takes place almost instantly so that at short distances from the source, lateral-line-mediated responses are quick and accurate. Beyond the immediate near field, the whole-body responses of the fish dramatically reduce the effectiveness of the lateral line; also, because of the rapid decrease in net acceleration, when the distance to the source becomes large relative to the fish's length, the stimuli for the lateral line becomes negligibly weak.

The pattern of stimulation (net accelerations) along the lateral line is very sensitive to the orientation of the fish relative to the sound source. In the case of schooling fish such as Sprat, it is known that the lateral-line system is very sensitive to changes in position or angle of the fish relative to the sound source. Small changes in position result in large changes in the pattern of stimulation of neuromasts. This sensitivity permits this schooling fish to respond almost instantaneously to the change in position of its nearest neighbors (Demon and Gray 1983, Gray 1984, Partridge and Pitcher 1980).

The orthogonal-like orientation of hair cells in otolith organs appears to support the idea that directional information can be obtained from the inner ear. Combined with the cosine response of individual hair cells, upon stimulus, the acoustic particle acceleration could be decomposed into components aligned along the directional axes of the otolith organs (Popper and Coombs 1982, Popper and Platt 1983, Saidel and Popper 1983). Other work has shown that fish compare the phases of acoustic pressure via the indirect stimulation route via the swimbladder, with the particledisplacement derivative of the sound field obtained directly. This permits resolution of the 180" ambiguity inherent in oscillatory motion (Schuijf and Buwalda 1980). It is not clear how the fish's central nervous system processes information about the impinging sound field to determine the location of the source, particularly in light of the complex directivities of natural sources where a vector analysis of the incoming sound field would not necessarily point to the source (Kalmijn 1988, Popper et al. 1988). It is reasonable to assume that, in the outer segments of the near field and into the far field, sound-field detection may only provide clues that permit the fish to guide itself to the source, although not localizing the specific site of the source until near enough for the lateral line to become operative. In the case of avoidance, it is possible for fish with good pressure-to-motion transduction capability to move down-gradient away from intense sources over distances up to several kilometers (Engas et al. 1993). Fish have also been observed to change their orientation in the far field of sources such as fishing vessels (Nunnallee 1991; E.P. Nunnallee, NMFS Manchester Lab., Manchester WA, pers. cormnun., Oct. 1993).

The mechanisms of sound localization by fish are not completely resolved. Investigations have shown that fish can localize sound sources, sometimes with very little information as in the case of very shortduration sounds. Mechanisms for localization at short distances, within a few body lengths, for sources with simple directivities appear more straightforward, the complication being that in nature there are very few monopole-like sound sources with simple near-field directivities (Schellart and Buwalda 1990). Theories for localization mechanisms at longer ranges, in the far field where the detection of acoustic pressure and utilization of phase relationships between pressure and particle motion appear necessary, are still in the early stages of evaluation. Regardless of our ability to discover the relevant mechanisms, species such as cod have been shown to have quite good sound-localization capability at longer distances from sources. For example, cod have been trained to discriminate differences in the azimuth and elevation of a sound source as small as 10" to 20". They have also shown the ability to resolve the 180" ambiguity inherent in oscillatory particle motion and the capability to discriminate sound-source distance over ranges of several meters (Buwalda 198 1, Buwalda et al. 1983, Schuijf 1975, Schuijf and Hawkins 1983, Blaxter 1988, Popper and Platt 1993, Hawkins and Sand 1977).

The contemporary view is that the lateral line is optimal for detection and response in the near field of sound sources where particle motions are largest and where the relative motion between water particles and the fish's body is maximized. In the far field, where the relative motion between particles and the fish's body is small, the inner ear performs localization functions. In the far field, the necessary information about the location of a source is contained in the motions of water particles and the amplitude and phase relations between particle motion and acoustic pressure. Acoustic pressure information is obtained through the effect on the inner ear by various pressure-to-motion transducers, such as swimbladders and prootic bullae, of some fish species. Information about the particle-motion component of sound fields is detected directly by movement induced in the otolith organs of the fish's inner ears (Fay 1988). It appears that those fish with functioning pressure-to-motion transducers have a very definite advantage in all areas, including the localization of sound sources.

Fish Sensitivity to Sound Frequency

As stated previously, the lateral line is mainly concerned with acoustic frequencies <200 Hz. However, the lateral line does not appear to be a passive sensory system; its morphology enables it to attenuate or amplify certain frequencies (Demon and Gray 1988). The morphology of the lateral line provides external clues to potential frequency response. For higher sensitivity to slowly varying transients or lower frequencies, large lateral lines are necessary. In addition, increased sensitivity to particular frequency bands can likely be achieved through compliant membranes covering lateral-line canals. In general, there appears to be a very wide range in the morphology and function of lateral lines. Not infrequently, a single fish may have a variety of lateral-line morphologies, with different types located in different body regions.

Neurophysiological response curves for the lateral line show highest sensitivities at frequencies toward the upper end of the organ's range for the species under study (Harris and van **Bergeijk** 1962, Muenz 1985, Sand 1981). However, it is well known that the lateral line is very important in detecting sources at very low frequencies, i.e., < 10 Hz. Measurements of the local flow fields generated by fish approaching and passing, as well as those stationary and hovering, have shown spectral peaks

below 10 Hz. As Kalmijn (1988) explains, the lateral line apparently acts as a "pre-whitening" filter, increasing in sensitivity with frequency at approximately the same rate that the spectra of the stimulus decreases with frequency. The result, when both factors are considered, is that the detectability of a source remains flat through the infrasound region (down to frequencies of 0.1 Hz or less; Dijkgraaf 1963) up to peak sensitivity, after which it falls off very rapidly. Using this analysis, Kalmijn (1988) has shown that the lateral-line system has strong "low pass" characteristics and that the sharp tuning shown in literature frequency-response curves, where displacement vs. frequency is plotted, is artificial and misleading when the detectability of a particular frequency is being considered. Kalmijn has shown that frequency response begins to fall at − 40 Hz for free neuromasts and − 80 Hz for lateral-line canal organs. This same argument holds true for the frequency-response curves for the inner ear that appear in the literature.

Studies have shown that many species can be trained to discriminate the frequency and intensity of pure tones and to detect tones masked by noise (Jacobs and Tavolga 1968, Fay 1970 and 1974, Tavolga 1974, Popper and Fay 1973 and 1984, Fay and Popper 1980). It is not entirely clear how fish can discriminate frequency. A combination of possible mechanisms is currently being considered: 1) temporal analysis of stimulus-generated spike rates, 2) regionalization of sensitivity to different frequencies in different otolith organ areas, 3) hair cells tuned to different frequencies, and 4) comparison of direct and indirect signals (Popper et al. 1988). The mechanism favored by these authors is (4). They argue that fish can use the same information for detection and discrimination of frequency as well as for localization of a sound source. In their model, since the indirect path is frequency-dependent while the direct path is not, the information to the central nervous system would be frequency-dependent, with components to permit frequency discrimination. One of the consequences of this model, if true, would be that fish without swim bladders or those with poor reradiation from their swim bladder would have poor ability to discriminate frequency. There is some evidence that this is the case (Tavolga 1974).

The frequency response of fish varies by species and, in general, is optimal between frequencies in the infrasound region (< 20 Hz) up to ~ 700 Hz (e.g., Platt and Popper 1981, Buerkle 1968, Chapman and Hawking 1973, Offut 1974). Although some species have been shown to respond to intense sound at frequencies as high as 150 kHz, frequencies well beyond the hearing of humans (Dunning et al. 1992, Nestler et al. 1992, NYPA et al. 1991ab, Boss and Dunning 1993), no physiological studies have been conducted at these frequencies and the potential mechanisms for response at these frequencies are not known. What is clear is that hearing at these high frequencies appears to run counter to all existing physiological data and theory.

Temporal Characteristics of Sounds
Important to Fish Response

The time-domain characteristics of sound-duration, rise time, pulsed or continuous-are also important in fish detection and response. Sounds of short duration must be louder for fish to become aware of them (Hawkins 1981). The question of what constitutes a short duration requires additional investigation, but fish have been shown to respond to air guns at transmission durations of 20 to 40 ms (Skaiski et al. 1992, Pearson et al. 1987 and 1992, Engas et al. 1993). Herring have been shown to respond to a single cycle as well as to a signal containing several cycles (Blaxter et al. 1981). Sounds that reach their peak in short durations tend to cause fish to exhibit a stronger alarm response than

sounds obtained via signals with longer rise times but equal peak sound levels (Schwartz 1985). In general, it can be said that temporal characteristics of the sound field do influence the ability of the fish to detect the sound and influence the fish's reaction to the sound; however, as in the case of all generalizations in fish hearing, there is considerable between-species variation.

It is clear, however, that the temporal characteristics of sound cannot be overlooked when fish behavior-modification systems are being developed. In particular, the crescendo wave form used by some (Loeffelman et al. 1991ab) is known to significantly raise response thresholds. Blaxter et al. (1981) showed that the response threshold of clupeids was raised by a factor of two when as few as four cycles were transmitted before the source reached full amplitude. They also observed that schools of herring would quietly swim past very intense sound sources of steady sinusoidal stimulation. Apparently the fish became habituated to the sound as it steadily increased in strength during their approach.

Sound Detection, Thresholds, Masking, and the "Cocktail Party" Effect

The level at which a fish can detect a sound is dependent upon the level of background noise. Studies by Tavolga (1967) and Buerkle (1968) found that sound must be at least 10 dB above background noise to be detected. Measurements of background noise were not made in many of the other early studies of fish hearing. For this reason, the results of these studies are not particularly useful, the lesson being that any study of fish hearing must consider background noise.

Studies conducted by Hawkins and Johnstone (1978) using Atlantic salmon showed that masking occurred in the far field when the spectrum level of noise approached within ∼ 24 dB relative to the hearing threshold of the fish. Masking can also occur from noise at frequencies other than the center frequency of the sound source. Some fish can filter out sound at frequencies differing from the sound it is attempting to detect. The capability to perform this filtering process is species-dependent. Cod are able to effectively filter out noise that is more than – 36 Hz on either side of the frequency of interest (Hawkins and Chapman 1975). Hawkins and Johnstone (1978) found that Atlantic salmon had a significantly lesser capability than cod to filter out noise. Atlantic salmon are not able to filter out noise that is less than ∼ 90 Hz on either side of the frequency of interest.

Fish are also known to use their ability to locate the sound source to discriminate against noise. This is known as the "cocktail party effect": the ability to use information about source location to discriminate against noise originating from other locations. It is an example of spatial filtering, whereby the directivity of the receiving sensory system is focused on the source of the desired signal excluding (to the extent that the directivity of the receiver permits) noise coming from regions outside the highest-gain portion of the receiver. Gains of 6-8 dB relative to the geometry of coincident signal and noise sources were observed in fish when the signal and noise sources were separated by at least 45" (Chapman 1973, Chapman and Johnstone 1974). Results of other studies also indicate that fish are capable of using spatial discrimination to maximize their ability to hear the noise of desirable signals (Fay and Coombs 1983, Fay and Ream 1986, Buwalda 1981). When spatial discrimination is considered, along with the fish's ability to discriminate and filter frequencies and utilize temporal

characteristics of signals, it can be concluded that fish have a number of signal-processing capabilities that permit them to discriminate desirable signals in the presence of considerable noise.

The background noise of the environment is not as important to salmonids as it is to species with better hearing, such as cod. Measurements of background noise in aquatic environments such as the ocean, lakes, and rivers have shown that the sensitivity of salmonids is so low that (except for extremely noisy environments, such as in the vicinity of waterfalls or the tailrace of dams), they are not limited by background noise but by the low sensitivity of their octavolateralis system. In contrast, species like cod (Hawkins and Chapman 1975) have such high sensitivities that, except under unusually quiet conditions, they are limited by background noise and not by the inherent sensitivity of their octavolateralis systems (Hawkins and Johnstone 1978).

Sound detection thresholds, background noise, and other characteristics of a sound source, and the receiving fish's sound sensory system must be specified in terms of the adequate sound-field stimulus for that species. Until very recently, most data of this type have been universally expressed in acoustic pressure referenced to one standard or another. Quite clearly this is not appropriate under near-field conditions for those species lacking pressure-to-motion transducers or in those cases where an octavola-teralis structure is present but is not functioning for such purposes. For salmonids, hearing thresholds and sound-field measurements must be expressed in terms of particle acceleration. It is of little value to have data expressed in acoustic pressure and have no direct, unambiguous means of translating these values to the component of the sound field stimulating the fish's sound sensory system. For example, it is quite clear that the adequate stimulus for the salmonid sound sensory system is particle motion, and that to obtain a spontaneous avoidance reaction the fish must be in the near field of the source (Knudsen et al. 1992 and 1994, VanDerwalker 1967). Assuming the monopole field equations (presented in Appendix A) would be appropriate for the source, one would still need to know the distance from the source at which pressure measurements were made to calculate an estimate of particle acceleration corresponding to the pressure measurement.

Development of Sound-Deterrence Systems: A Historical Review

Investigations of the reaction of fish to sound have been conducted since the mid-1800s and recently have experienced something of a revival, as fish stocks continue to decline and tools permitting multiple uses of water become urgently needed. These investigations have been of two types: biological engineering and physiological research. Biological engineering efforts are focused on solving a particular problem, such as reduction of entrainment of smolts in operating flows. The term "biological engineering" first appears in the literature in published comments of Dr. van Bergeijk, following a 1967 presentation by VanDerwalker of the response of salmonids to low-frequency sound.

Physiological investigations have been concerned with the mechanisms of hearing in fish, evolutionary biology, etc. This work has resulted in an extensive literature providing valuable information about fish hearing systems and their relationship to sound fields. However, specific information is available for only a very small number of fish species of economic importance or those amenable to laboratory experimentation.

The two approaches are complementary rather than competitive. Both provide essential information, and both should be included in efforts to develop sound-deterrence or behavior-modification systems. They converge at the level of controlled experiments under free-field conditions, and case studies of both are discussed in subsequent sections.

Biological Engineering: The Early Years

The essence of the biological engineering approach is (1) exposure of test fish to sound at various discrete frequencies or bands of frequencies, intensities, and presentation patterns, and (2) observation of fish for spontaneous avoidance responses, typically called "startle" responses by investigators. The search is for something that "works," and the criterion is a response that can be used to deter, exclude, or in some other way modify fish behavior. Typically the mechanism of the response is not sought.

The desirability of using non-intrusive methods for reducing the entrainment of downstream migrating salmon and steelhead in turbine flows at Columbia River dams was identified over 40 years ago (Collins 1954). Sound was one of the stimuli that were evaluated. Initial studies were funded by the Army Corps of Engineers and conducted by the Fish and Wildlife Service (Moore and Newman 1956, Burner and Moore 1962, Burner and Moore 1953 and 1962). These studies used biological engineering approaches with the objective of finding sound stimuli that would evoke avoidance responses in salmonids. Underwater acoustic devices developed during World War II were used to generate and monitor sound fields. Engineering and scientific expertise was combined with the skills of fishery biologists to design and conduct various experiments. However, neither of these studies were successful in finding a stimulus that elicited an avoidance response from salmonids.

The early studies were truly "shots in the dark." One obvious reason was that information about the fish octavolateralis system developed over the 40 years since then was not available, rendering experimental design (selection of frequencies, sound field levels, the relevant stimulus for the lateral line and inner ear) essentially impossible. Severe problems were encountered in constructing

enclosures that would permit experimentation at low frequencies (i.e., <5OO Hz). Generated sound fields were not well defined, and standing-wave and other boundary effects prevented characterization of the elements of the sound field to which the test fish were exposed. Observations made in natural environments, such as lakes and the ocean, encountered problems with high levels of natural back-ground noise. In many cases the sound intensities tested, while thought at the time to be very intense, are now known to be considerably less intense than that required to obtain avoidance responses in salmonids. These studies, while worthy early efforts, provide little useful information, although they did report what is now termed a "spontaneous awareness reaction" to low-frequency sound. What is interesting, perhaps ironic, is the number of studies presently being conducted with designs that mirror these early efforts, and with equally unlikely prospects of providing positive results.

VanDerwalker's experiments

Improvements in experimental design were made by VanDerwalker (1967), who conducted both field and laboratory experiments. His field experiments are particularly interesting. He replicated an experiment conducted by the California Department of Fish and Game to guide juvenile chinook salmon and striped bass into a bypass channel. No information about these studies is available in the open literature, but from VanDerwalker's account they were initially successful and then failed when repeated.

VanDerwalker constructed a sound barrier diagonally across a loft-wide irrigation canal with an adjacent 5-ft bypass channel located in eastern Oregon (Figure 9). The sound barrier consisted of a series of ten 3x 4ft steel plates mounted vertically and parallel to the water flow. The plates were mechanically driven at a frequency of 270 Hz resulting in a sound pressure of 123 **dB//μPa@1m** at a distance of 1 ft upstream of the plates. The presence of the plates alone increased the proportion of downstream migrating steelhead entering a bypass channel. During operation of the sound barrier, the
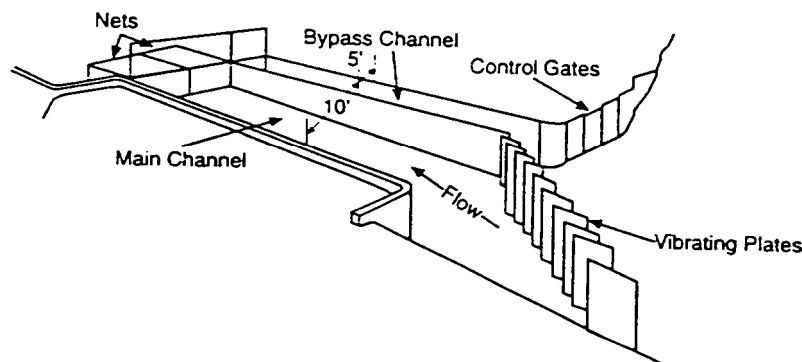

Figure 9. VanDewalker's sound barrier system and evaluation facilities in irrigation canal near Umatilla, Oregon (modified from VanDerwalker 1967.)

percentage of fish entering the bypass doubled. This was a remarkable experiment, and it is not clear why further development was not pursued, or, if pursued, not reported. In the light of current knowledge, we know that 270 Hz is near the upper end of the sound sensory range of salmonids where sensitivity falls very rapidly, and that the sound levels generated were probably too low for maximum effectiveness.   In the latter regard, however, at the frequency the plates were driven, the sound-pressure measurements were made in the near field and are, therefore, undoubtedly a poor measure of the portion of the generated field to which the fish were most sensitive (i.e., particle motion).

In his laboratory studies with juvenile chinook salmon, VanDerwalker constructed a rectangular endless raceway and attached anechoic chambers. He pumped water through the raceway at a velocity of one-half ft/sec. Using an electromagnetic vibrator driving a 6-inch disk bonded to a rubber gasket, he was able to generate frequencies over the range of 10 to 500 Hz at levels up to 156 **dB//μPa@** lm. He monitored the generated field using a pressure-sensitive hydrophone located 2 ft in front of the sound source. His findings have strong similarities to the most current physiological and behavioral work to be described later (Knudsen et al. 1992 and 1994). He found that juvenile chinook salmon responded at all frequencies tested up to 280 Hz, with no response noted at higher frequencies. His quantification of fish response based on various criteria showed essentially level response from 35 to 170 Hz, dropping markedly on either side of this range. All responses were obtained within the near field of the sound source, and the sensitivity of the fish to repeated exposure did not decrease. He found that nearly all fish reacting to the sound swam laterally away from the source. In his paper he does not note whether the fish were hatchery or wild.

VanDerwalker documented the difficulty of experimenting with low-frequency sound in a small tank (his "anechoic" chamber turned out to be not very anechoic) and suggested that future experimen-tation be done in a free-field environment or that a major effort be made to develop an anechoic test facility. His results follow clearly from what we now know to be the primary stimulus for the salmonid octavolateralis system, i.e., particle motion and not acoustic pressure. The sound field measurements he made of acoustic pressure are not very useful in understanding the levels of particle motion to which the fish responded. In the near field, whereas sound pressure falls off as the inverse of distance, the net acceleration along the fish's lateral line fails off as the inverse of distance to the fourth power. This means that even over very short distances, the relevant stimulus field will decrease considerably while minor decreases in sound pressure will take place. The result is that sound-pressure measurements do not describe the level of the relevant stimulus and, because of the complexity of the sound field due to the geometry of the source and other factors, there is no simple mathematical expression that can be used to estimate particle acceleration as a function of distance given sound pressure.

EPRI studies

Beginning in the late 1970s and continuing through the 1980s, the Electric Power Research Institute (EPRI) funded studies to review and assess power-plant intake technologies, including behavioral barriers. The behavioral barrier technologies included sound but were primarily motivated by successes documented by Ontario Hydro researchers using light to attract and repel fish (Patrick 1982, 1983, 1984, 1985; Patrick and Vascotto 1981; Patrick et al. 1982, 1985, 1988; Haymes and Patrick 1984, 1986; LMS 1988; McKinley and Patrick 1987b). In the final report of the advanced intake

technologies study, Stone and Webster Engineering Corporation (EPRI 1984, 1986) drew the conclusion that low-frequency sound had been extensively investigated and proven ineffective. However, the studies cited are those discussed previously in this paper which are clearly flawed for a number of reasons, and the analysis on which the conclusions were based was not documented. Also, Stone and Webster's review did not include the extensive physiological literature which would have placed the reviewed studies in context. However, in the same report, following statements of the ineffectiveness of sound to stimulate avoidance behavior in fish, Stone and Webster listed pneumatic poppers, low-frequency sound sources used in seismic exploration, and water jets (another source of low-frequency sound) as showing promise and requiring further evaluation. The report's conclusions, including the summary analysis of promising behavioral barrier technologies relative to sound, are contradictory and were based on a very narrow cross-section of the total spectrum of information available at the time.

The EPRI advanced intake technologies study laid the groundwork for evaluation of strobe lights, mercury lights, hammers (low-frequency sound sources), and two proprietary sound-generating systems at a number of hydro plants located across the United States. These studies were conducted in 1987 and 1988 and reported in an interim report in 1990 (EPRI 1990). The report summary states that only a slight, temporary avoidance was obtained for juvenile American shad using sound. Strobe lights were quite consistent in eliciting avoidance responses from several species, including chinook and coho salmon and steelhead. The response to mercury lights was more equivocal.

The EPRI studies represent the zenith in biological engineering. Considerable effort was expended to obtain participation from a cross section of the hydropower community and to focus the studies on those fish species causing the most significant passage challenges for hydropower plants. Once past this point, the effort focused on getting equipment into the water and attempting to measure fish response. The results of the field studies were ambiguous for the reasons later cited by Dunning et 'al. (1992): "full-scale tests at operating power plants can be very expensive, do not readily permit direct observation of fish, and are affected by variations in target species and environmental conditions." The complexity of studies under field conditions cannot be overemphasized: A myriad of environmental factors influence fish behavior on an hour-by-hour basis; tools and procedures to monitor the behavior of test subjects are not well developed; and meaningful controls are not easily or inexpensively accomplished.

The EPRI studies also included laboratory experiments with the hammer low-frequency sound sources, consisting of a spring-loaded mass and a metal plate enclosed in a steel drum. These experiments are worth considering because of the fish species tested (Atlantic and chinook salmon, rainbow trout, and alewife) and because of their similarities to the early studies of Moore and Newman (1956). The studies were conducted in a concrete pool 51 ft square and 5 ft deep, with a liner of open concrete block to help reduce reflections. Fish were released into the center of the pond and allowed to acclimate for at least 30 min. Following acclimation, the fish were exposed to sound from hammers (a spring-loaded mass and a metal plate enclosed in a steel drum) located in opposite corners of the pool and operated sequentially for periods of 30 min each. The spectral content of the sound field was modified by changing the thickness of the steel plate struck by the device's sliding mass (hammer). The distribution of fish within the pool was observed by video cameras and quantified.

Differences between control and test conditions were not observed, and the investigators concluded that the sound fields had no effect. The experimenters referenced the high variability in the behavior of test fish under control conditions (no sound) as an element in their inability to detect

differences in behavior under test conditions. Clearly the experiments were capable of detecting only the most obvious behavioral responses. In addition, and perhaps more significantly, reference to the physiological and other literature would have predicted this result. Salmon and trout have been shown to be responsive to particle motion, not to sound pressure, and to have significantly reduced sensitivity at frequencies > 200 Hz. The distance from the hammers, given their source levels (– 190 dB//μPa@1m) at which particle acceleration would likely have stimulated an avoidance reaction, would have been a few feet, probably less that 10 feet, the dimension of one of the 25 cells in the pool within which fish behavior was being observed. For alewife, a species well equipped to detect acoustic pressure, it is likely that the sound-pressure field within the pool was very complex, due to reflections from the boundaries, and did not provide choices for the fish. For example, reflections from the air-water interface (which undergo a 180" change in phase resulting in modification to the sound field through addition) and the depth of the pool would have acted as a filter, in effect removing a portion of the low-frequency end of the spectrum from the propagating signal. There are many other possibilities for the failure of such experiments, but these alone are sufficient to conclude that the results of these experiments cannot be considered the definitive work regarding the response of salmonids to low-frequency sound.

New approaches

In short, the types of studies implemented in the EPRI field and laboratory experiments with sound do not permit the control required to draw clear conclusions, either positive or negative. Probably the net benefit from these studies was to motivate a different approach to biological engineering studies. Interest in sound as a component of behavioral barriers was maintained through this experimental stage by some successful applications, including that of Ontario Hydro (Haymes and Patrick 1986) at the Pickering Nuclear Generating Station on Lake Ontario where pneumatic poppers appeared to reduce by 99% the entrance of alewives to an experimental structure. LMS Engineering used another device very similar to hammers, mechanical fish pulsars, to successfully divert alewives into a bypass at the Hells Gate Hydroelectric Station on the Black River (LMS 1988b). These successes were balanced by failures of poppers to reduce impingement of alewives, American shad, and blueback herring at the Roseton Generating Station on the Hudson River (LMS 1988a) and the failure of fish pulsars to consistently elicit an avoidance response from American shad at the Annapolis Generating Station on the Bay of Fundy. Regardless of the failures, the feeling of many was that it was clear that fish used sound in day-today living and that if the "right" frequency could be found, behavioral barriers using sound would be possible.

The new approach to biological engineering was demonstrated by the Army Corps of Engineers in their studies to develop behavioral barriers for blueback herring at the Richard B. Russell Dam on the Savannah River and those of the New York Power Authority for alewife at various electric generating stations on the Great Lakes and elsewhere. The essence of this new approach was to first conduct controlled experiments in field laboratories under free-field conditions where the test stimulus could be highly controlled, the responses of the fish clearly observed, and undesirable sound field conditions avoided. These tests would then be followed, if warranted, by field-scale experiments. The steps of this new approach were to 1) identify a sound stimulus that elicits a response from a species of interest, 2) evaluate whether the obtained response, if effectively replicated under field conditions, could be reasonably expected to result in a desirable outcome (i.e., repulse fish, etc.), 3) specify the features of

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the sound system that would be required to deliver the effective stimulus and evaluate its cost/benefit, and **4)** if steps 1 through 3 are concluded satisfactorily, conduct field studies at operating power-production facilities. In the biological engineering approach, no effort is made to determine how the fish detect the sound or any aspect of the mechanisms leading to a response. In addition, typically only responses that result in active swimming movement of the fish are of interest. It is also important to note that up to the present, investigations have focused on far-field responses, the idea being to attempt to influence the behavior of fish at relatively large distances from power plant intakes. There are many species of fish, including salmon and trout, for which this strategy has been unsuccessful in the past and most likely will prove unsuccessful in the future.

A modification of the new biological engineering approach as defined by the studies of the Army Corps of Engineers (COE) and the New York Power Authority (NYPA) has been pursued by the American Electric Power Service Corporation (AEPSC). In their approach, sounds made by test fish are recorded and analyzed, and a complex signal resulting from that process played back into the water using moving coil transducers (Loeffelman 1990, Loeffelman et al. 1991ab, Hanson Environmental Inc. 1993, Cramer et al. 1994). The theory of this approach is that fish are vocal, and that vocalizations from captured fish will contain elements of sound (frequency, duration, amplitude) that are matched to the sound sensory systems of others of that species. Many fish species are known to emit sounds (Schneider 1967, Myrberg 1981, Hopkins 1988, Tavolga et al. 1981), which consist mostly of frequencies < 3 kHz made in a number of ways, including rubbing of various structures and drumming of the swimbladder. Sounds are known to be produced by some fish species when approached by a predator, as those resulting from the tail flips of avoidance reactions (Stober 1969) and grunts or sounds resulting from the deployment of defensive displays (Hawkins 1986). Such sounds are known to communicate at certain levels. Some fish are apparently able to discriminate vocalizations by their own species (Hawkins and Myrberg 1983). Stober (1969) observed avoidance response by other rainbow trout stimulated by one individual's tail flip. Other studies (Tavolga 1958) have shown that fish will respond to playback of recorded calls, although other studies have shown that sounds are only one component of a complex assemblage of visual and other behavioral stimuli required for response (Hawkins 1986). Many sounds are a component of reproductive behavior (Gray and Winn 1961).

The use of sounds emitted by fish as a means of obtaining biologically meaningful sound stimuli to elicit responses is in the early stages of evaluation. The approach has been field-tested to divert adult steelhead trout from migration up a fishladder and downstream migrating chinook salmon smolts and steelhead trout from entering fyke nets deployed in the forebay of a hydropower plant (Loeffelman et al. 1992). Results of these tests indicate that diversion did take place. However, in tests of the 1992 method at Tracy, California, no definite, repeatable reactions to sound signals were observed for northern squawfish, yearling coho salmon, striped bass, steelhead trout, subyearling chinook salmon, channel catfish, and threadfin shad (pers. commun.: John Ferguson, COE, Portland OR; Carl Schilt, AScI, Trotters Shoals SC; John Nestler, COE, Vicksburg MS). Evaluation of this approach continues at irrigation diversions in California (Hanson Environmental Inc. 1993, Cramer et al. 1994) with mixed results.

The experiences of the NYPA and the COE in the following case studies offer insight into the types of studies, their sequence, and the time required to systematically develop effective behavioral barriers. Both of these development efforts are based on observations by Bendix Corp. and South Carolina Wildlife and Marine Resources Division personnel in the mid-1980s. During operation of an acoustic fish-counting device at Stevens Dam, South Carolina, blueback herring showed a strong avoidance

response to high-intensity (source level = 200 dB//μPa@ 1 m) 120-kHz sound (Al Menin, formerly of Bendix Corp., Sylmar CA, pers. commun. 1990). In these tests, some blueback herring within -6 ft of the sound source were **stunned** or killed.

Case Study 1: The Corps of Engineers develops a sound-deterrence system for the Richard B. Russell Hydropower Project.

The COE began investigating the effects of sound on blueback herring and shad (both clupeids) at the Richard B. Russell (RBR) Dam on the Savannah River in Georgia in the fall of 1988. The following historical development is from Pickens (1992) and Nestler et al. (1992).

In the first tests performed in the fall of 1988, shad, bluegill, and bass were placed in a rectangular-shaped net and ensonified (Figure 10). Avoidance responses by shad were obtained at frequencies around 120 kHz. Based on these encouraging results, the COE spent the winter of 1988/89 upgrading their equipment to more easily facilitate experimentation over a range of repetition intervals, frequencies, burst speeds, and amplitudes, and to increase the maximum source levels of their sound system.

Background noise at RBR was measured in February 1989 and determined to be 50 dB//μPa@ 1 m lower than the maximum source levels of the 120-kHz sound system ($\sim$ 190 dB//μPa@1m), which indicated that the sound source could transmit signals at 120 kHz that would not be masked by background noise.

A series of tests was conducted in April 1989 using herring, shad, and trout. Testing in the 60 to 500 Hz range produced initial reactions from the herring and shad, but they seemed to quickly acclimate on repeated exposure. The trout were not observed to react to any stimulus during the
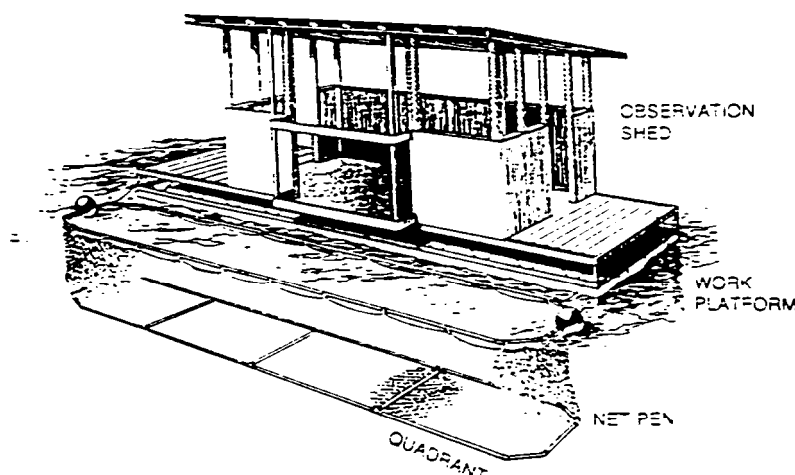

Figure 10. Sound evaluation facility, including net-pen for holding fish during testing, floating work platform and small observation shed. (Modified from Nestler et al. 1992.)

experiments. In addition to showing avoidance behavior, the herring and shad were attracted to a continuous 80 Hz signal which resulted in speculation about the possibility of attracting these species away from danger zones using sound.

High-frequency experiments were also conducted in April 1989, using the same setup as at low frequencies. Herring and shad showed definite avoidance reactions when test frequencies approached 100 to I10 kHz. These behaviors seemed at their peak at frequencies around 130 kHz. Continuous random noise over a band of 100 to I50 kHz also produced strong avoidance behavior. Further experimentation determined that a 130-kHz signal of 176 dB//μPa@1m would cause the herring and shad to move at least 25 ft. Higher power was subsequently tested, and it was determined that at source levels of 183 dB//μPa@1m, effective ranges of at least 200 fi could be obtained. Additional experiments with lights during this same time-period determined that mercury or sodium lights would attract herring and shad, raising the possibility that combining the attraction power of light with the repulsion power of sound might enhance the effectiveness of sound or light alone.

The first level of field-scale experimentation was conducted in June 1989. Acoustic work in the RBR tailrace showed that the behavior of the herring population and, indirectly, of associated species could be modified on a project scale with high-frequency sound. Tests showed that fish could be excluded for distances up to 300 ft from the transducer within the ensonified volume with source levels of ~ 180 dB//μPa@1m. However, it was also discovered that the fish acclimatized after continuous pulsed transmission for about I hour. This indicated that the sound systems would have to be flexible so that frequency and other features of sound transmissions could be altered frequently to avoid acclimatization by the fish. Based on experiments conducted during the summer, the COE procured enough equipment in the winter of 1989 to ensonify the entire region in front of the RBR intake tubes out to a distance of 300 ft from the dam and developed controllers for the sound system to provide the required operational flexibility. Also during the winter of 1989, the sound fields generated by sound system transducers were modeled, and analysis of the placement of transducers and their operation to optimize coverage of the region in front of the intake tubes was conducted

The prototype sound system was installed by April 1990. However, problems with the system components prevented operation as specified, delaying system activation until August. During testing following activation of the prototype system, sound was transmitted at frequencies of 118 kHz, 125 kHz, and 132 kHz in sequence for durations of 15 min with cycle times of IO sec on and 5 sec off; during the "on" portion of the cycle, 5 msec transmissions were sent every 50 msec. Under these operating conditions, no evidence of acclimatization was observed over periods of 7 to 8 hours.

Hardware and operations problems with the sound system were worked on during the winter of 1990/91, but operation in July 1991 encountered new problems. Low water levels in the tailrace caused the transducers to be located under the thermocline. Herring, which tend to locate just above the thermocline, were not dispersed by the sound system. It was determined that floating transducer mounts would be required to permit sound to be transmitted into the region of the water column containing the fish. Additional challenges were encountered during 1991 that resulted in realization that many site-specific characteristics had to be considered, any one of which could cause the system to become ineffective. After considerable effort to modify the system, operation of the system in 1991 resulted in almost complete movement of blueback herring and shad from the tailrace within 200 ft of the dam for considerable periods of time.

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At the present time, the system is deployed at full scale and has been in operation since July 1993. The system has performed very well during this time, with the result that entrainment of fish has been reduced to negligible levels. Development of the core of the system required 4 years, and additional time will be required before operations under a range of environmental and plant operating conditions are experienced and the system has been fully exercised over the full range of expected conditions. As of the end of 1993 the total costs for development of the system, including equipment, were about $2 million. This represents a small fraction of the $34 million that the bar screens planned for the facility would have cost without any assurance that they would have solved the problem.

Case Study 2: The New York Power Authority develops a sound-deterrence system.

The New York Power Authority (NYPA) has had a sustained interest in reducing entrainment of fish at their power production facilities. Species of particular interest at the Indian Point Generating Station are white perch, Atlantic tomcod, and striped bass. The alewife was the species of particular interest at the James A. FitzPatrick Nuclear Generating Station located on Lake Ontario near Oswego, New York.

Beginning in 1987 and continuing into 1988, following mixed success with various low-frequency sound sources at other power production facilities (Haymes and Patrick 1986, LMS 1988ab and 1989), the NYPA conducted a test of hammers (low-frequency sound sources consisting of a spring-loaded mass and a metal plate enclosed in a steel drum) at their Indian Point plant located on the Hudson River. The tests resulted in a decrease in the number of fish in the vicinity of the power plant intakes. Encouraged by these results, NYPA (funded by the Empire State Electric Energy Research Corporation) sought a means for increasing effectiveness and flexibility. To accomplish these objectives, an electronic fish-startle system was developed and tested during the winter of 1988-89 at a quarry. The initial quarry studies showed strong avoidance responses by white perch and striped bass to high-amplitude sound at frequencies < 1 kHz under daylight conditions. However, the avoidance responses decreased under low light and did not occur during darkness (NYPA et al. 1991a). These results indicated that higher intensities might be required under conditions of darkness to elicit avoidance behavior in the target species.

The quarry studies were similar to the cage studies being performed concurrently by the COE (see Case Study 1; Nestler et al. 1992). Fish were held in a large cage (Figure 11) where their behavior could be visually monitored as they were presented with acoustic stimuli. As mentioned previously, testing fish for behavioral responses under modified and observable field conditions is a major addition to the new biological engineering approach and fundamentally distinguishes the new approach from that of the EPRI studies, etc. In the case of the COE experiments (Nestler et al. 1992), it was discovered that blueback herring showed a strong avoidance response to intense high-frequency sound (I 30 kHz, I40 dB//μPa@1m) and that, under field conditions, American shad and gizzard shad also seemed to respond to intense high-frequency sound.

The results of the COE experiments suggested to NYPA that tests of high-frequency sound (i.e., > 100 kHz) might elicit strong avoidance responses from alewives. They also wanted to perform elicit avoidance responses from juvenile white perch and striped bass. Additional studies were
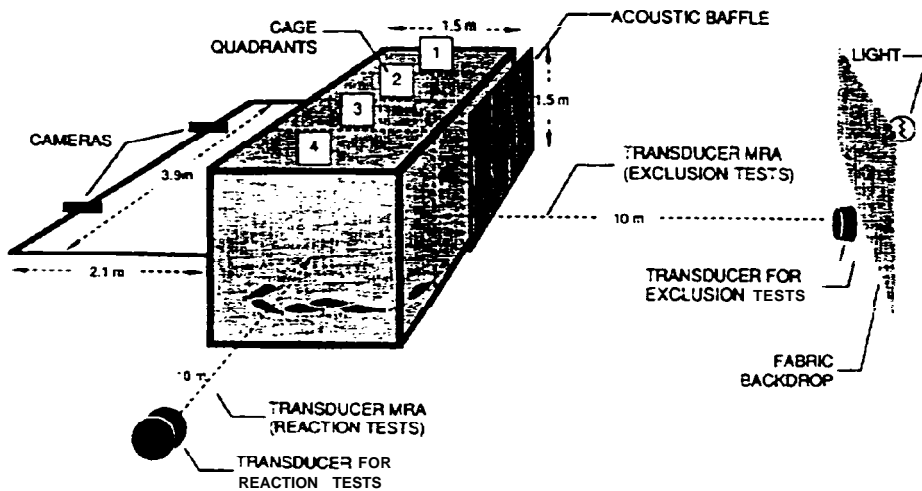
Figure 11. Orientation of cage and its quadrants, transducers and their maximum response axis (MRA), light, fabric backdrop acoustic baffle, and cameras for testing (modified from Dunning et al. 1992)

additional testing with low-frequency sound to determine if intense low-frequency sound would conducted in the winter of 1989 at the quarry where young-of-the-year (YOY) white perch, YOY and yearling spottail shiner, YOY and yearling golden shiner, YOY and yearling striped bass, yearling and older alewives, and adult Atlantic tomcod were tested. These tests found that alewives habituated to pure tones but consistently showed avoidance to intense pulsed broadband sound (117-133 kHz; 163 dB//μPa@1m). The alewives did not habituate to the broadband sound over exposure periods up to I50 min. Night responses were weaker than those observed during daylight. The white perch, striped bass, Atlantic tomcod, golden shiner, and spottail shiner did not respond to the high-frequency sound. During the day, white perch and striped bass showed a strong avoidance response to low-frequency sound (broadband < I kHz; 148 and I60 dB//μPa@ Im) and at night a weaker response to more intense sound (191 dB//μPa@1m) over the same frequency band. Atlantic tomcod, golden shiner, and spottail shiner exhibited only a weak avoidance response to low-frequency sound (NYPA et al. 199lab, Dunning et al. 1992).

An important addition to the field testing conducted in the winter of 1989 came out of observations during the first quarry studies (conducted a year earlier) that test fish suffered from holding and did not exhibit consistent responses to sound stimuli. Therefore, to control the effects of holding and other factors from tests, test fish were exposed to sound stimuli known to be effective in eliciting a strong avoidance response prior to subsequent testing. These 'reactance" tests helped assure that tested fish were healthy enough to be reactive to test stimuli. Reactance testing appears to be an important addition to the new biological engineering protocol.

The quarry studies. or rather interpretation of them in the context of general fish biology, provided additional critical information, i.e., the expectation that the response of fish, their "reactiveness" to sound, was most likely a function of physiological state which in turn resulted from basic biological rhythms as well as factors such as degradation in condition due to capture and holding. The poor fish

response during darkness was finally understood as the result, largely, of the general decreased activity of fish moving into behavior patterns typical for winter, when feeding activities and activity patterns in general were considerably different from pre-spawning spring activities when peak impingement (90% May-June) occurs. This assessment of test results, rather than the one that appeared most obvious, turned out to be valid. In the broader context of fish response to sound, it is clear that fish "reactance" is a function of physiological state and that physiological state has temporal rhythms and can be negatively impacted by study conditions.

The quarry studies were followed in the spring of 1990 by the first phase of feasibility testing of a high-frequency sound system (122-128 kHz) to reduce impingement of alewives in the cooling water intake of the James A. FitzPatrick Nuclear Power Plant (JAF) on Lake Ontario. The objectives of this first phase were to test the assumptions and obtain site-specific information upon which elements of the design and conduct of a full-scale feasibility test would be based, to test the tools and methods required to monitor a full-scale test, and to obtain additional information on alewives and other fish in the vicinity of the intakes. The feasibility test found that (1) acoustic conditions at the site were suitable (low background noise at 125 kHz and low reflections from the surface and bottom that might destructively interfere with the transmitted deterrence signals), (2) mounting locations for system transducers and other equipment were available and equipment cables could be routed to avoid damage, (3) fish response in the vicinity of the intake could be monitored acoustically and visually (the capability to qualitatively and quantitatively monitor was confirmed through deployment and extended use of monitoring equipment), and (4) large numbers of alewives moved onshore into the intake area each night and offshore away from the intake area during the day. The presence of high numbers of fish was considered essential for an unequivocal test of sound under field conditions.

The phase-l portion of the feasibility study was followed in the spring of 1991 by phase 2, design and fabrication of a full-scale prototype deterrence system, and phase 3, a field test of that system. The deterrence system was designed using site information obtained during phase 1 and facility engineering documentation. An element of design was sound-field modeling to determine the number and characteristics of transducers required to fully ensonify the intake structure openings. The final design called for I6 narrow-beam (25" circular) and 4 wide-beam (96° horizontal by 72" vertical elliptical beam) transducers. The system was operated at a duty cycle of 0.5 sec pulses of broadband high-frequency sound (122-128 kHz) every second. The source levels of system transducers were I90 dB//μPa@1m (i.e., sound pressure level at distance of lm from the source). Fish strongly avoided high-frequency sound at a distance > 80m from the intake. When the nuclear reactor was operating and warm water was discharged through a diffuser offshore of the cooling water intake, the system reduced the number of fish in the vicinity of the intake by as much as 96% and reduced alewife impingement by as much as 87%. However, when the reactor was off, the reduction in impingement fell to 27%. The investigators speculated that the thermal discharge was acting as a barrier to the alewives, preventing their approach to the back side of the intake. Since there were no deterrent-system sound sources on the back side of the intake, the alewives could approach the intake from the back and enter the intake circumventing the deterrence system (Ross et al. 1993). Additional transducers were added to the back of the intake in the spring of 1993. Under "down" reactor conditions and no thermal discharge that resulted in reduced deterrence system effectiveness in the 199 1 study, the 88% decrease in impingement observed in 1993 confirmed the hypothesis that alewives had been approaching the intake from the back in 1991.

The relationship between aspects of operation at JAF, environmental variables, and fish behavior on the effectiveness of the prototype deterrence system confirms the conclusions of the LMS (1989) report that the high variability in results of application of behavior-modification devices were apparently related to environmental conditions at test sites. Boss et al. (1993) also make the point that if they had not considered wind direction, time of day, reactor operation, and lake temperature in their data analysis, they would not have been able to determine that alewives consistently avoided the sound fields created by the deterrence system. The 1993 tests confirmed that post-spawning fish are not very reactive and would not provide an accurate test of the system. However, the effect of the system was clearly evident when alewives were most abundant.

At present, a permanent sound-deterrence system is being planned at JAF for late 1996. While the effectiveness of a full-scale deterrence system has been demonstrated under operating conditions, adoption of new technology for permanent installation at a major power-production facility requires considerable engineering and planning. The testing otacoustic effects on fish behavior began in 1987 and led to the full-scale FitzPatrick feasibility tests in 1991. Four years were required to proceed from controlled observational experiments of fish response to sound to the final stages of full scale feasibility experiments leading to specification of a viable fish deterrence system for a single nuclear generating station, and it was two more years before full-scale testing could be replicated in 1993. It appears that three additional years will be required before a permanent fish deterrence system is installed (Dermis Dunning, NYPA, White Plains NY, pers. commun., April 1994).

Lessons learned

Evolution of the biological engineering approach has resulted in several valuable lessons that can guide future efforts in its use. The first lesson is that there are no "overnight" successes. Both case studies began with chance observations that led to strong, consistent responses. Even with this "head start," the tasks of 1) confirming the fish response of interest under controlled conditions, 2) feasibility studies to determine whether physical features of the site were amenable to deployment of a sound system, 3) development of field-scale monitoring capability, and 4) fabrication, installation, testing, and debugging of a full-scale sound-deterrence system, all take years and not months. The time required for a sounddeterrence system is not outside that required for physical barriers or other fish protection systems (consider the ongoing development of submerged traveling screens); the point being that protection systems using behavioral tools are unlikely to take less time to develop than other types of fish protection systems.

A second lesson is that fish response to sound varies among species and that environmental conditions, including factors such as morphology of the site, water current patterns, seasonal stratification, and turbidity, among others, can influence performance of the system both from the standpoint of the physics of sound in water and the physiological response of fish to sound.

The second lesson leads to the third: that field-scale monitoring capability is absolutely necessary throughout all phases of development, from acquisition of baseline information on abundance and behavior of the target species, through installation and testing of the full-scale system. In the two case studies, physical capture, visual (direct observation and video), and hydroacoustic monitoring methods were necessary for development. The extension of this lesson is that, unless monitoring capability is

available or resources are allocated to develop the necessary capability, it is unlikely that a sound-deterrence system can be successfully developed. In fact, initiation of system development for site- and species-specific applications is not warranted unless it becomes clear that monitoring capability with necessary temporal and spatial resolution exists or has the high probability of being developed within a reasonable time-frame and at reasonable cost.

The final lesson from the biological engineering approach is that long-term operation of a full-scale acoustic deterrence system has not yet been achieved, and optimistic pursuit of such capability over a broad spectrum of species and sites is premature. The successful development of acoustic fish-deterrence capability documented in the two case studies is very recent and has been shown only for a subset of fish species with rather remarkable adaptations for detection of sound. A high level of skepticism appears warranted that similar results with similar levels of resources within a similar time-frame can be achieved.

Physiological Research

Undentanding the mechanisms of fish hearing

The physiological approach to identifying fish responses to sound that might be used for deterrence or behavior-modification systems for fish protection at water-control facilities is even more recent than the new biological engineering approach. What is meant here is that while the tools and methods of physiological research are not very new, the focus of the experimentation is new, i.e., toward identification of spontaneous avoidance responses that might provide the foundation for further development of a sounddeterrence system. The physiological approach differs from biological engineering in that the approach to "discovery" of a stimulus that will elicit an avoidance response flows from a more detailed analysis of the fish octavolateralis system. The other distinguishing characteristic is that in the physiological approach, efforts are made to understand the physiological basis for observed responses. The physiological approach has not be-en used in the United States in the past and is not currently being used largely because I) the large consumers of fish protection devices, i.e., private and public electric power companies and associated institutions, have been reluctant to fund work that looked like "basic research," and 2) those involved in such research have not shown pointed interest in the application of their work to fish protection needs.

Although at this time there is only one research group (Knudsen et al. 1992, 1994) that is using the physiological approach in the sense of the definition above, there have been numerous physiological studies of the fish octavolateralis system; however, the results have not been extended to conditions of an operating power plant or other water-control facility. However, the Knudsen et al. studies are extremely important because they deal with salmonids, fish with considerable economic and social value for which behavior-modification sound stimuli have been vainly sought for almost four decades. The objectives of the studies, conducted in Norway with funding from the Norwegian Water Management Association, were to evaluate the possibility of using intense sound as a deterrent to juvenile Atlantic salmon at hydropower production facilities and other water-control facilities such as irrigation diversions.

Case Study 3: Norwegian researchers clarify basics of salmonid sound deterrence.

As in the case of biological engineering, the goal of Knudsen et al. (1992) was to discover a stimulus that would cause a sustainable, spontaneous avoidance reaction by a target species of fish. The starting point of their investigation was detailed review of the physiological literature and use of current theory of the physiological basis for hydrodynamic and sound-field detection by fish. This is markedly different than the approach taken by the COE and NYPA (case studies 1 and 2) where follow-up on chance observation of a response by herring to intense high-frequency sound led them to discover stimuli for a deterrence system for related species. It is important to note that reliance on the physiological literature would not have led to discovery of the response of clupeids to high-frequency sound. In conversations early in development of the R.B. Russell deterrence system, well-known fish physiologists were incredulous that experimentation with high-frequency sound would be considered for such a use (John Nestler, COE, Vicksburg MS, pers. commun.).

Following the argument of KaJmijn (1988), Knudsen et al. recast the data for the hearing threshold of Hawkins and Johnstone (1978) in terms of particle acceleration. This showed what-many other studies of salmonids had inferred, that the "optimum" frequency for salmonids shown in terms of acoustic pressure by Hawkins and Johnstone was, in reality, the upper limit for the optimum range of sound detection by these fish. The recast hearing threshold indicates essentially a flat threshold from the infrasound region to – I50 Hz, above which the threshold rises steeply with loss of detection capability at > 380 Hz (Knudsen et al. 1992). Based on this analysis, Knudsen et al. selected 5, 10,60 and I50 Hz as test frequencies for the initial phase of their experiments. Also based on the results of previous research of salmonid hearing, emphasis was placed on particle motion and not on acoustic pressure. Salmonids have been shown to be considerably less sensitive to acoustic pressure than other tested swimbladder-bearing fish, being more similar to non-swimbladder-bearing fish in their hearing capabilities (Hawkins and Johnstone 1978). Hawkins and Johnstone (1978), in their discussion of the hearing mechanism of salmonids, conclude that "the swimbladder plays no part in the hearing of the salmon."

In the first phase of experimentation, Knudsen et al. determined the particle acceleration levels at which test fish showed spontaneous awareness of sound stimuli. The test chamber was a standing-wave acoustic tube designed to permit generation of uniform particle movements throughout the length of the tube and estimation of particle movements from piston displacements. Awareness was detected by measurement of fish heartbeats and opercular movements using electrodes external to the fish. Wild salmon parr and brown trout were tested. These experiments showed that spontaneous awareness reactions for the salmon and the trout were a function of frequency and were considerably above hearing thresholds. The lowest measured awareness thresholds at 5 Hz were ~ 25 $dB//10^{-5}ms^{-2}$ above the estimated hearing threshold of ~ 22 $dB//10^{-5}ms^{-2}$. At I50 Hz, the awareness threshold was ~ 73 $dB//10^{-5}ms^{-2}$ above the hearing threshold of ~ 15 $dB//10^{-5}ms^{-2}$. Thus at 150 Hz, the spontaneous awareness threshold for the test fish was $\sim 41 dB//10^{-5}ms^{-2}$ above that at 5 Hz. It was also found that habituation for salmon required a single exposure at 150 Hz and six exposures at IO Hz. Both salmon and trout showed the same trend in habituation.

Spontaneous-avoidance response was tested in a pool at 10 and 150 Hz on hatchery and wild Atlantic salmon parr. The sound sources were driven so that at a range of 2.5 m, sound levels were close to awareness-reaction thresholds. In all cases, the IO Hz sound caused spontaneous-avoidance reactions for fish within 2 m of the source. At this range, sound field values were > IO dB $//10^{-5}ms^{-2}$

above the awareness threshold. Beyond this range, no avoidance behavior was observed. Habituation was not observed after 20 repetitions within 3 to 4 hour test periods. Based on these tests, the authors suggest that particle accelerations at 5 to IO Hz should be at least $10^{-5} ms^{-2}$ to elicit an avoidance response.

A difference in avoidance response was noted between wild and hatchery fish. The wild fish always swam in the direction of increasing depth, whereas the hatchery fish on all occasions swam laterally directly away from the sound source without regard for depth. The authors speculate that hatchery fish may be conditioned in aspects of their avoidance behavior. They also suggest, when behavioral barriers are implemented, that thought be given to the likely avoidance path of the fish. At no time in the pool experiments were avoidance reactions to 150 Hz sound observed, even at levels 30 dB $//10^{-5} ms^{-2}$ above awareness thresholds.

The experience gained in these laboratory studies was applied at a small river located near Oslo, Norway, to test the use of intense low-frequency sound as an acoustic barrier to migrating Atlantic salmon smolts (Knudsen et al. 1994). In this study two frequencies were tested, 10 and 150 Hz. Smolts entering the test area consistently displayed a strong avoidance response to the 10 Hz sound. The effective range appeared to be approximately 3 m within which sound intensity was greater than $10^{-2} ms^{-2}$. Behavioral responses to the 150 Hz sound were not observed even at ranges less than 10 cm where sound intensity was greater than $4 ms^{-2}$, about 114 dB above the measured hearing threshold for Atlantic salmon at this frequency (Knudsen et al. 1992, Hawkins and Johnstone 1978).

The study reported by Knudsen et al. (1994) demonstrates that deterrence of migrating Atlantic salmon smolts is possible at small scales using 10 Hz infrasound. It is reasonable to expect that similar responses might be obtained for Pacific salmonids. However, controlled laboratory and small-scale field studies similar to that conducted in Norway have yet to be conducted within the Columbia River Basin on Pacific salmonids. Experimentation conducted recently at slightly larger scales in the Sacramento River in California targeted on Pacific salmonids (Loeffelman et al. 1991ab and 1992, Cramer et al. 1994, Hanson Environmental Inc. 1993) has shown promise; however, the need to follow the patented signal-conditioning technique at the core of these studies, which usually involves incorporation of signal elements at frequencies considerably above those shown effective by Knudsen et al. (1992, 1994), has not been proven. Given the simplicity and clarity of the Knudsen et al. (1994) demonstration, it is reasonable to consider that any deterrence demonstrated by these other efforts may be due to low-frequency components produced unintentionally as a byproduct of the instrumentation and signalconditioning techniques. Such distinctions will undoubtedly be very important, since the scale of operation required for fish deterrence systems at facilities such as mainstem Columbia River Basin dams may require rather extensive arrays of sound sources. If this proves to be the case, simplicity of construction and operation in addition to low cost will be essential requirements for the inwater elements (sound sources, cable, etc.) of such systems. Such requirements will be much more difficult to meet if complex signals requiring a broad range of frequencies, including high-intensity infrasound and complex signal-conditioning methods, are found to be necessary.

Salmonid response to sound: Conclusions from 40 years of investigation

There are important parallels between the physiological and biological-engineering approaches. The spontaneous-awareness thresholds shown in Case Study 3 are similar to the "reactiveness" testing performed in biological engineering. Also, the physiological state of the fish appears to be very important, as evidenced in Case Study 3 by the influence of rearing history on fish response whereas in case studies 1 and 3 other aspects of fish physiological state (e.g., reactiveness effected by capture and holding) proved important.

The Knudsen et al. (1992, 1994) studies are important because they bring to focus, and hopefully to conclusion, 40 years of effort to find a sound stimulus for a salmonid acoustic-deterrence system. These studies have strong similarities to the laboratory and small-scale field studies of VanDerwalker (1967) conducted almost 30 years ago and who also found avoidance responses at low frequency by juvenile chinook salmon. For the juvenile chinook in his studies, awareness and avoidance dropped off at frequencies > 150 Hz and remained level to frequencies down to 30 Hz. Response was flat over that range. The range of avoidance response was short, 2 ft, and the fish did not become less sensitive on repeated exposure. Almost all other studies conducted have sought avoidance responses at long range. One of the few exceptions is the study by McKinley and Patrick (1987a) in which sockeye salmon smolts were diverted from a fyke net by a low-frequency sound source located 1 m in front of the net opening.

There are a number of possible reasons why salmonids have not responded to sound at ranges greater than a few meters. However, the most obvious reason based on the physiological literature is that particle motions at these ranges are below the levels eliciting avoidance behaviors. The results of Knudson et al. (1992), viewed from the context of the many negative experiments of the response of salmonids to sound, lead to the conclusion that if salmonids are to be deterred by sound then such deterrence will be possible only at short ranges using very low frequencies. Among the positive benefits of short-range deterrence are the prospects of low habituation and broad applicability across several salmonid species and age groups. There are undoubtedly many beneficial uses for salmonid sound deterrence, even under these seemingly restrictive conditions.

The conclusions that salmonids respond to particle motion in the near field of low-frequency sound sources, among other topics, leads to speculation about other fish protection devices. Submerged traveling screens have been found to be the source of low-frequency sound within the region where salmonids exhibit awareness and avoidance reactions (Anderson et al. 1989). Computer models (Anderson 1988) and empirical evidence (Hays 1986, 1987) indicate that hydraulic considerations alone cannot account for the low intercept percentages by submerged traveling screens of juvenile salmonids entering turbine intakes. The characteristics of particle motion, particularly particle acceleration, within the immediate vicinity of a source is such that a strong gradient in the stimulus field is present. This field contains sufficient information for salmon to direct their movement along gradients that would expedite their avoidance of the screens. If this is true, then it is unlikely that purely hydraulic considerations will result in screen designs that will achieve intercept ratios otherwise considered achievable without other negative side effects, such as increased strike rate with resulting higher descaling.   Studies recently reported by Nestler and Davidson (in press a,b) indicate that smolts may be responding to hydromechanically-generated sound fields in the vicinity of within-turbine screens at mainstem Columbia River dams. A potential benefit of investigating the sound fields of within-turbine

screens would be information to (1) help in the design of large-scale sound sources that influence salmonid behavior or (2) provide feedback to the engineering design of water-control facilities such that fish response to facility features are considered.

The differential behavior of wild and hatchery fish, and larger and smaller fish, are also reasons for concern in the design and implementation of fish protection devices that might emit low-frequency sound fields. The tendency for wild fish to 'sound' (i.e., move into deeper water) when avoiding such fields, whereas hatchery fish tend to move laterally, could bias captures toward hatchery fish (Knudsen et al. 1992). Inclined plane traps-riverine sampling gear with characteristics somewhat similar to submerged traveling screens-have been shown to be selective for smaller fish, capturing age-0 and age-l sockeye smolt in much higher proportion than age-2 smolt (Ken Tarbox, Alaska Dep. Fish & Game, Soldotna AK, pers. commun., June 1994). Downstream migrating smolt have been visually observed to enter fyke nets, then swim out and down against the current to escape capture by going under the net (Pat Roe, Bonneville Rower Admin., Portland OR, pers. commun., April 1994). Almost everyone who has ever worked with physical capture gear can report similar results and observations. The main argument for such selectivity has been that the better swimming ability and greater endurance of larger fish permit them to avoid capture at a higher rate than smaller, less physically capable, fish. While this is most likely a major factor, it is also likely that better deve!oped lateral-line and inner-ear sensory systems of larger fish provide for earlier detection and permit significantly longer reaction time and distances. In particular, larger fish with longer lateral lines are thought to have a sensory advantage over smaller fish, since it is net accelerations along the lateral line that indicate the direction and distance of a sound source (Kalmijn 1988). It is also possible that the sensory capability of fish increases as the fish matures. There is some evidence that this is the case (Blaxter and Hoss 1981).

Findings and Discussion

The last ten years have seen major advancements in understanding the mechanisms of the fish octavolateralis system. Also during this time, sound-deterrence systems for the exclusion of clupeids from the intakes of a nuclear and a hydropower plant have been developed and demonstrated. These advances have laid the foundation for further development of sonic behavior-modification systems. However, very significant challenges remain. Some of the more significant of these developments and challenges, as they relate to the Columbia River Basin Fish and Wildlife Program, are considered in the following sections.

Fish have highly evolved sound-sensory systems

The fact is that all fish use the information contained in sound to increase their chances of survival. Current theory and experimental results support the conclusion that most, perhaps all, fish have a three-dimensional perspective of their environment through their ability to detect and analyze sound. The history of physiological research has shown that anthropomorphic arguments do not lead in directions that provide much help in understanding the mechanisms of the octavolateralis system of fish. One of the more interesting examples is goldfish which are able to discriminate between sound that differs in phase, and are thereby able to differentiate between sounds that are first sensed as a compression and as a rarefaction (Fay 1982). Humans (terrestrial animals in general) do not have this capability.

Physiological studies have also shown that there is considerable difference in capabilities even within groups that appear morphologically similar. An example is salmon and cod, both swimbladder-bearing fish but with differences in structure and placement of the swimbladder relative to the inner ear. The result is that salmon have hearing like that of non-swimbladder-bearing fish, sensitive only to particle motion, whereas cod are more like the 'hearing specialists" with special structures and sensitivity to acoustic pressure. The lesson here is that when sound is generated in water, we can expect different portions of the fish community to react differently. A concern when implementing sound-deterrence systems is to avoid negative responses and maximize positive ones.

Are sound-deterrence systems feasible? Yes and maybe.

Experience with clupeids by two different research groups developing sounddeterrence systems has shown that sound can be used to reduce entrainment of fish in flows at power-production facilities. Their experiences have also demonstrated that there are considerable technological, biological, operational, physical, and acceptance complexities involved in the development and implementation of these systems. Development times and costs of sound-deterrence systems appear to be consistent with those of other fish-protection devices. However, recent experience (see case study 2) shows that very large cost savings are possible when fish behavior modification can be used instead of physical barriers.

Although the feasibility of sound-deterrence systems for some species and sites is clear, it is also important to realize that experience with sound-deterrence systems is very short-lived and that the technology, while mature at the component level, is very immature at the system level. Caution is advised in broad extrapolation of experience with a particular species at a specific site to other sites with the same species or to other species at the same or different sites. This caution should sound familiar to those with experience working with any fish-protection system, physical or behavioral.

Sound-deterrence systems development in the Columbia River Basin

First Step: Ask the "right" questions. In order to maximize the benefits of research and development investments, it is necessary to clearly frame the problem being approached before initiation of work. This appears to be especially true in the case of sound-deterrence system development. If an avoidance response is sought, it is necessary to define the specific application and specify the response necessary to achieve the desired objective. It is also necessary to have the best information possible in describing the behavior of the target species at the target site under current conditions and the stimuli that appear to be driving those behaviors. For example, if the objective is to modify the behavior of fish approaching traveling screens, it will be necessary to characterize the sound field generated by the screens and to determine if current fish behavior is in response to those fields.

At the present time, the questions being asked are of one type: What stimulus will evoke an avoidance behavior that can be used to develop a fish-dispersion or deterrence capability? However, another question requiring research and development is: If it is desirable to influence the behavior of predators, might it be much more effective to ask whether flooding their sensory systems with biologically meaningful sound that would interfere with their ability to detect prey might be more effective than dispersion? Other deterrence options are also worth considering, e.g., dispersion in combination with sensory-system blocking might prove the most effective of all.

Regardless of the primary objective of research into the reaction of fish to sound, it is important to be aware of the fact that sound transmits extremely well in water and that the potential for impacts well beyond the target species may not be desirable. For example, sounds generated to disperse predators may also impact the species for which protection is sought.

The necessity of both physiological research and biological engineer@. The present state-of-the-art of biological engineering and physiological approaches to development of sound-deterrence systems is the result of evolution over the past several decades. Both approaches are disciplined and, when focused on the "right" questions, should aid development of deterrence and behavior-modification capability or quickly and methodologically identify problems impacting feasibility. However, these approaches require a high level of discipline, experience, and use of sophisticated tools. It is quite unlikely that researchers unfamiliar with this discipline will be effective in these areas without considerable investment in training and tools.

The two approaches have their individual strengths and, while either could eventually result in full-scale behavior-modification systems, it is likely that a combination of the two approaches will provide the best return on investment and the shortest path to implementation of full-scale systems when

feasible. The physiological approach will be required to develop hearing thresholds and similar basic information about species of interest. The biological engineering approach will be required to scale up from laboratory to field scales.

An example for which contributions from both approaches will be required is squawfish, a predator of considerable importance to salmon recovery, with special adaptations (Weberian ossicles) that should permit excellent hearing both in terms of acoustic pressure and particle motion. Without basic information on the hearing capability of squawfish, it is unlikely that consideration of the full range of possibilities to influence the behavior of this species, using sound to the benefit of downstream migrating salmonids, will be possible. In addition, the wide range of sites at which modification of squawfish behavior might be desirable will require considerable biological engineering.

The "adequate" sound stimulus: An essential ingredient for success. Lack of clear recognition of the adequate stimulus for salmonid response to sound has resulted in a large unproductive investment in research and development over the last several decades. Initially the lack was of physiological information to point the direction. However, this void was filled with the work of Hawking and Johnstone in 1978. They quantified the frequency range of sensitivity and clearly demonstrated that particle motion, not acoustic pressure, was the adequate stimulus for salmonids. While another critical piece of information was still missing, the information they provided should have resulted in a considerably different approach to salmonid sound-effects research in the 1980s. Although their results were widely cited, they were not used beyond selection of test frequencies and, even there, considerable liberties were taken. The critical missing piece, that at the systems level the lateral line and inner ear are particle-acceleration detectors, was provided by Kalmijn in 1988 and immediately put to use by Knudsen et al. (1992, 1994).

When the history of sound-effects research on salmonids is reviewed, one thing becomes clear: There appears to be a disconnect between the physiologists and those implementing the biological engineering approach. It is likely that the expediting of linkage between the two approaches would provide a very significant and immediate return on investment. The detailed knowledge of the physics of underwater sound as it relates to fish hearing, so convincingly demonstrated by prominent physiologists, is not reflected in biological engineering. Likewise, the detailed knowledge of fish-protection needs and the realities of full-scale operations well known to biological engineers is not displayed by physiologists.

Clear identification of the adequate sound stimulus for a fish species, and equally clear linkage with the physics of sound fields derived from disciplines applied by physiologists, are necessary to well-founded sound-effects research. In addition, this knowledge must be integrated at the core of biological engineering research and development efforts to maximize the return on investments in these efforts.

The Columbia River Basin: So little information . . . So many needs. There is very little, if any, specific information for many species within the Columbia River Basin of importance to salmon recovery. The best general information readily available is for salmonids. However, even for the-se species. there are very important information needs. The literature indicates that there are behavioral differences in avoidance responses between hatchery and wild fish. It also appears that significant differences may exist in the sound-sensory systems of small and larger fish, which may translate into between-species differences due to varying sizes at smoltification, or within-species differences

between fish at different stages of smoltification. Even if attempts to develop capabilities to influence the behavior of salmonids was never begun, it seems that issues related to the potential effects of sound fields generated by fish-protection devices currently in use (submerged traveling screens) should be investigated. Such work **would,** of necessity, address some of these information needs. In addition, if submerged traveling screens generate sound fields that are effective in modifying salmonid behavior, their study would result in information useful in developing devices for a wide range of applications.

At this time, there is no information in the open literature about the sound-sensory systems of squawfish or other significant predators. Testing of related species has indicated very highly developed sound-sensory systems with low detection thresholds, sensitivity to acoustic pressure, wide frequency sensitivity, narrow masking filters, and good source-location capability (Hawkins 1981, 1986); in other words, all capabilities that make for effective predation in situations where the sensory systems of salmonids would be overwhelmed.

Sound fields to which Columbia River fish are exposed are essentially unknown. Only one attempt has been made to systematically survey a portion of the underwater acoustic environment of the Columbia River (Anderson et al. 1989). Unfortunately, all measurements were made with pressure-sensitive hydrophones, and there is no way to accurately translate these measurements into the measures of particle displacement that salmonids detect. This is because of the multiple sources, site characteristics, resulting complex sound fields, and the non-linear relationship between acoustic pressure and particle displacement in the near field of the low frequencies that dominate the measured sound fields.

What seems clear is that better knowledge at fairly high spatial resolution, relative to known fish distribution patterns, in the near vicinity of the various water intakes, etc., will be required to evaluate the feasibility of fish behavior-modification systems. It is also likely that even more detailed information of the acoustic environment will be required if the development of acoustic behavior-modification capability reaches the point of full-scale deployment and testing. At the present time, it seems that the rigor required in sound-field characterization for fish behavior-modification systems (particularly for those species sensitive to particle motion, such as salmonids) will likely require innovation, perhaps considerable innovation. Acoustic pressure measurements have been sufficient for development of almost all underwater sound systems for military or civilian use. Only infrequently has work in the near field been critical to the functioning of a system. This will most likely not be the case for fish behavior-modification systems.

Expect complications and ambiguity. The experimental evidence is very clear: The response of fish to sound depends on several factors that must be considered during development of behavior-modification systems. Experience has shown that fish responses to sound stimuli will vary with species, age, physiological state, prior conditioning, and environmental variables.

The data from sound behavioral experiments also leads to findings that are very significant for the Columbia River Basin Fish and Wildlife Program and for recovery plans of endangered stocks. One finding of significance is that hatchery fish appear to be conditioned by their rearing history such that their response to sound stimuli differs from that of wild fish. Given the importance of wild fish in the recovery of Columbia River stocks, it will be necessary to first verify that such differences exist for Columbia River fish and, if verified, to better characterize the differences and try to understand what they might mean within the context of fish behavior-modification system development.

A second finding of significance is that smaller, less mature fish appear to have lower sensitivity to sound than larger, more mature fish. Differences in basic sensory capability such as this could be very important in determining the specifications of sound behavior-modification systems. The implications of such basic sensory differences to other aspects of the downstream migration of salmonids, even in the absence of sound modification systems, are not clear and warrant further thought.

Sound sensory systems of fish can be disabled by gas bubble disease. The sensory systems of migrants can be negatively impacted by environmental conditions, making them unable to detect and respond to sound. Research has shown that gas bubble disease can impair the lateral-line system of steelhead trout and, under some conditions, render the system insensitive (Weber and Schiewe 1976). It is likely that the lateral line of other salmonids and perhaps other species responds similarly. The significance, beyond that to sound behavior-modification systems, is that fish rely on sound to warn them of the approach of predators and to help them sense and interpret their physical environment. Loss or impairment of the lateral line or other components of the octavolateralis systems could significantly impact the survival of these fish.

The open literature contains no information about the effects of other common diseases on the octavolateralis system. In general, fish disease research does not include evaluation of sublethal impacts of fish disease on fish sensory systems.

Prospectus

It can no longer be argued that acoustic fish protection at some power-production facilities is unfeasible. However, it is not clear that sound can be used to help protect downstream migrants at mainstem Columbia River dams. Successful fish deterrent systems have not been clearly demonstrated for Pacific salmonids, and research has shown that avoidance responses will most likely be obtained only from salmonids at short distances from sound sources and at low frequencies and high intensities (Knudsen et al. 1992, 1994). The idea that the behavior of salmonids can be influenced by sound at long ranges, as proven feasible for clupeids, does not appear viable. These limitations require rethinking about how, when, where, with what technology, and at what cost Columbia River downstream migrants might be presented with a stimulus to achieve deterrence or other behavior modification. On the positive side, recent research under small-scale field conditions has demonstrated that Atlantic salmonids consistently exhibit an avoidance response to infrasound (Knudsen 1994).

The necessary tools and methodologies to investigate the feasibility of fish behavior-modification in the Columbia River Basin have been demonstrated. However, their implementation will require an integrated program that makes use of both physiological research as well as biological engineering. The goals of such a program must be carefully thought through and clearly specified to make the best use of time and resources. The experience of the recent past tells us that such a program will require a minimum of 4 to 5 years, that it will cost several millions of dollars, and that there are no assurances of success. However, the cost and time for development are well within the bounds of developing other fish-protection devices. In addition, recent experience has shown that successful application of sound for fish protection can result in significant installation and operational savings.

There is a lack of information about sound fields in the Columbia River in general, and particularly those in the immediate vicinity (near field) of power intakes and devices such as traveling screens. In addition, there is a lack of physiological and behavioral information for species other than salmonids. These deficiencies will extend the time and cost of feasibility evaluation as well as implementation of full-scale systems.

The fact that acoustic pressure measurement will likely prove insufficient to adequately characterize the particle-motion components of sound fields that are the primary stimulus for salmonids adds another level of complication. Measurement of displacement and its derivatives in areas such as turbine intakes or the vicinity of traveling screens will require innovation in measurement instrumentation and will be very difficult to perform.

The suggestion that wild and hatchery fish respond differently to sound is troublesome given the need to avoid impacts to wild fish. Before any full-scale behavior-modification system is installed, it will be necessary to demonstrate that wild fish are not negatively impacted given observations that their avoidance response to sound is apparently to swim toward the bottom. Also, if the hydropower system is manipulated in the future so that gas supersaturation occurs, it is well to remember that the sound-sensory systems of salmonids can be debilitated or disabled following exposure to such conditions.

Regardless of the complexity and ambiguity of fish behavior, the high cost and continuing challenges of physical fish-protection systems encourage continued investigation of ways to influence

the behavior of fish. While Columbia River dams present what is likely the ultimate challenge to such endeavors, there are many applications, smaller in scale and much less complex, wherein the probability of successfully implementing behavior-modification systems is quite high. If all else fails, these applications in and of themselves would probably provide a good return on the research and development investment made at mainstem dams.

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Appendix A:

Physics of Sound Fields

Simple sound sources

Monopoles

Characteristics of sound fields depend upon the nature of the source. One class of sources-monopoles (pulsating spheres)-creates sound fields similar to those generated by piezoelectric or other transducers for conversion of electric to acoustic energy (Figure A. 1). Transducers, which operate at frequencies above the hearing range of most fish (> 5 kHz), are an element of the echo sounders commonly used by fishermen to aid them in locating fish. At these frequencies, the gas-filled swim-bladders and the bony parts of fish are very efficient reflectors of sound. The reflections of the transmitted sound from the fish can be used to detect the fish and note their location. High-quality echo sounders are also used to quantitatively assess abundance and distribution and to observe the behavior of fish populations (Kanciruk 1982, Venema 1985). Classical conditioning experiments with salmonids at the frequencies used for fish assessment have shown that they are unable to detect sound at frequencies typically used for fish assessment (Facey et al. 1977). However, it is known that some species such as clupeids are sensitive to frequencies as high as 150 kHz, which includes the lower end of the range typically used for fish assessment in freshwater (120 to 500 kHz) and encompasses essentially all of the range used for fish assessment in marine water (20 to 120 kHz).

The equations describing the sound field generated by a monopole source (the simplest of sound sources) as presented by Kalmijn (1988) are summarized below.

$$p = -(\rho c k a^2/r) U_0 \sin(\omega t - kr) \qquad\qquad 1.0$$
$$v = -(k a^2/r) U_0 \sin(\omega t - kr) + (a^2/r^2) U_0 \cos(\omega t - kr) \qquad\qquad 1.1$$

Where:

ω = angular frequency = $2\pi c/\lambda$
t = time
v = particle velocity
d = particle displacement
U_0 = amplitude of radial source velocity
a = radius of pulsating sphere
r = radial distance
p = acoustic pressure
ρ = ambient density
ω = wavelength
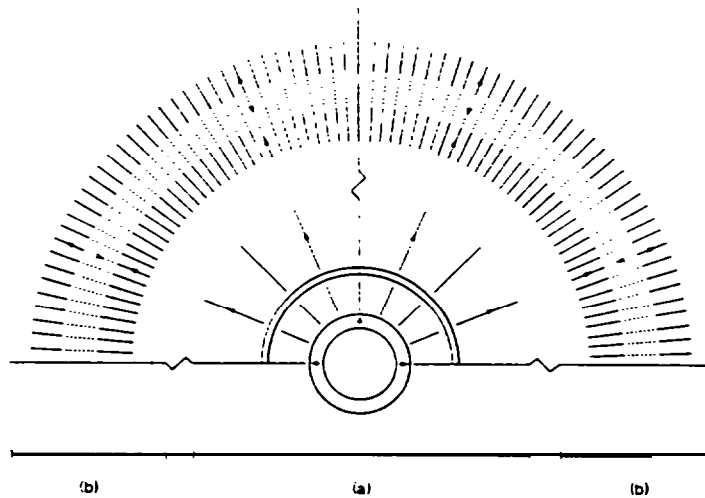k = wave number = ω/c
c = speed of sound

Figure A.1. Monopole field of a pulsating sphere. (a) Local-flow field is centered on the source and ndially symmetrical. Water occupies increasingly larger, but thinner, shells as it moves outward. Particle velocities fall off as $1/r^2$. (b) Propagating sound wave is also centered on the source and radially symmetrical. Particle velocities fall off as $1/r$. Arrows indicate sense of the particle velocities; heavy shading denotes compression; light shading denotes rarefaction. (From Kalmijn 1988, p. 87; used with permission.)

There is much to be learned from study of these equations. However, for our purposes the most important factors are understanding that the monopole sound field is not directive and that it consists of two components. The **near field** dominates very near the source where particle motions have the characteristics of hydrodynamic flows in which particle motion dominates; and **the far field** dominates farther away from the source where particle velocity and acoustic pressure are characteristic of a propagating sound wave. The two components are shown in equation 1.1 where the second term represents the near field. The significance is that only in the region near the sound source are water-particle motions sufficiently strong to directly stimulate the fish lateral line or inner ear.

The second term of equation 1.1 can be used to understand an important feature of the near field. The particle velocity of this portion of the sound field falls off as the range squared. This means that the primary stimulus for the lateral line will become negligible within a few body lengths of the source. The effective range for direct stimulation of the inner ear extends beyond that of the lateral line because of its coupling (through the otolith) with the water. Through indirect stimulation via the swimbladder and special adaptations, the effective range of the inner ear is extended into the source far field. In physical terms, the extent of the near field for monopole sources is $\lambda/2\pi$, where λ is the wave length.

Physical descriptions of sound fields are mainly useful in appreciating how the components of sound relate to the fish's sensory systems. They cannot be used to estimate the ranges within which the lateral line and inner ear might be directly or indirectly stimulated for a particular species. This sort of information can be obtained only through experimentation with the species of interest. However, once the capability of a species to directly and indirectly sense and respond to a sound field is known, the

source-field equations can be used to predict and evaluate the potential performance of different sources to generate sound fields with specific properties. However, caution is in order even for this purpose. Very few of the sound sources typically used to generate sound fields for fish-hearing research, or to stimulate a specific fish response, are classical monopoles. For example, typical transducers are directive and generate near fields that do not behave in strict accordance with the field equations.

Dipoles

These rigid, constant-volume, vibrating spheres create fields that more resemble those generated by moving fish (Figure A.2). Such fields differ from monopoles in several significant ways, one of the more important being the geometry of the generated field. Monopoles are radially symmetrical, meaning that the axis of the vibratory motion of water particles points to the source. This is significant when considering the question of localization of sources by fish. Dipole fields are considerably more complex. Only within a very narrow angular range along the axis of vibration of the sphere and at short distances do particle motions point to the source. This means that, except at short ranges (on the order of a few body lengths), it is unlikely that fish can move directly to a source following clues obtained from water-particle motion. Alternatively, they may use the sound field to guide them in an
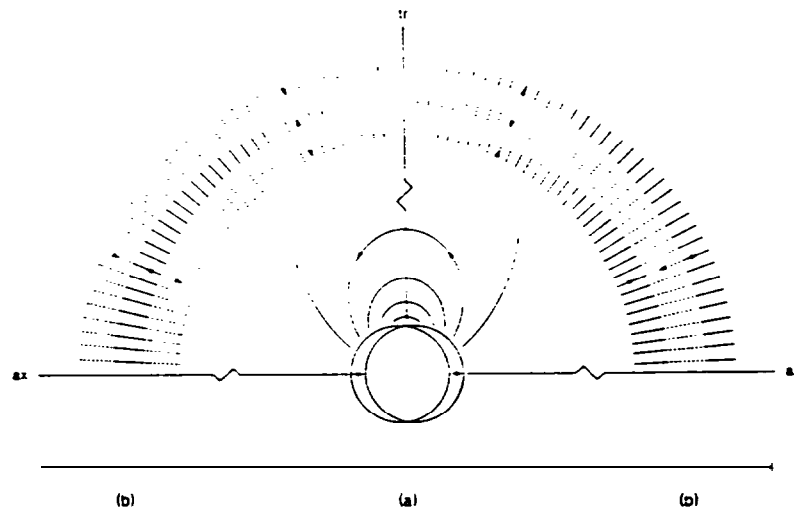

Figure A.2. Dipole field of a vibrating sphere. (a) Local- and intermediate-flow fields are not centered on the source. except along axis of vibration, and are not radially symmetrical. Field lines begin and end at surface of the sphere. Particle velocities fall off as $1/r^3$ and $1/r^2$ respectively.
(b) Propagating sound wave is centered on the source, but is not radially symmetrical. Particle velocities fall off as $1/r$, being strongest along the axis of vibration and zero in the transverse plane. Arrows indicate sense of the particle velocities; heavy shading denotes compression; light shading denotes rarefaction; ax = axis of vibration, tr = transverse plane. (From Kalmijn 1988. p. 94; used with permission.)

indirect searching mode toward the source and into the very near field where particle motions point more directly to the source. In nature, with the possible exception of swimbladders, there are few monopole-like sources; rather, the vast majority, resulting from the whole-body motions of fish, are dipole-like.

As in the case of monopoles, sound fields generated by dipoles are dominated very near their source by hydrodynamic flow. Within this portion of the sound field, displacement, velocity, and acceleration decrease in proportion to the cube of distance from the source. This is a significantly higher rate of decrease than that of the monopole near field. However, in keeping with their greater complexity, dipole fields have a transition between the inner portion of the near field and the far field where the rate of decrease with distance of the relevant quantities become proportional to the inverse of distance squared. The far field of a dipole decreases proportionally to the inverse of distance as does that of a monopole. In physical terms, the near field of a dipole-that region where the particle velocity of the local flow and that of the sound wave are equal-is 1.4 $\lambda/2\pi$ along the axis of vibration, increasing at larger angles and increasing to infinity at 90° where the propagating sound wave goes to zero.

The equations describing the sound field generated by a dipole source as presented by Kalmijn (1988) are given below.

$$P = -(\rho ck^2a^3/2r)U_1\cos\theta\cos(\omega t-kr) - (\rho cka^3/2r^2)U_1\cos\theta\sin(\omega t-kr) \qquad 1.2$$

$$v_r = -(k^2a^3/2r)U_1\cos\theta\cos(ot-kr) - (ka^3/r^2)U_1\cos\theta\sin(\omega t-kr)$$
$$+ (a^3/r^3)U_1\cos\theta\cos(\omega t-kr) \qquad 1.3$$

$$V = -(k^2a^3/2r^2)U_1\sin\theta\sin(wt-kr) - (a^3/2r^3)U_1\sin\theta\cos(\omega t-kr) \qquad 1.4$$

Where:

ω = angular frequency = $2\pi c/\lambda$
t = time
v_r = radial particle velocity
v_θ = tangential particle velocity
d = particle displacement
U_1 = amplitude of axial source velocity
a = radius of vibrating sphere
r = radial distance
P = acoustic pressure
ρ = ambient density
λ = wavelength
k = wave number = ω/c
C = speed of sound
θ = the angle of radiation relative to the axis of vibration

Comparison of the field equations for monopoles and dipoles provides insight into the increasing sound-field complexity as sound sources become more similar to those most likely to be encountered in nature. The field equations for dipoles show clearly that we can expect that most natural sound sources will not have uniform directivity. They also indicate the sound-field complexity with which the fish octavolateralis system must cope to perform its various functions.

A.4

Measurement of sound fields

The primary challenge of sound-field measurement occurs in the near field, where particle displacements are significant and where the directivity of the source may be very complicated. In most experimental situations where measurements are being made in enclosed spaces with both hard and soft boundaries, there are additional effects that complicate the sound fields (Hawkins and MacLennan 1976, Parvulescu 1967, van den Berg and Schuijf 1985).

Most sound-field measurements in both the near- and far fields have historically been made using hydrophones that are pressure-sensitive only, the reason being that transducers to measure particle displacement were not readily available. The sound field near the source cannot be accurately characterized by the use of pressure-sensitive hydrophones. Regardless, many investigators have measured pressure in the near field and used the following equation by Harris (1964) to estimate particle displacement even though it is accurate only for an ideal monopole source in a free sound field, which is rare in nature.

$$d = @/(23rf@c)))(l + (\lambda^2/(2\pi r)))^{1/2} \qquad\qquad 1.5$$

Where:
- d = particle displacement in cm
- P = sound pressure in **dynes/cm^2**
- f = frequency of sound in Hz
- λ = wavelength in cm
- r = distance from the source in cm
- (ρc) = medium acoustic impedance typically estimated to be 1.54 E 05 **g/cm^{2}s**

(Particle displacements estimated using this equation are frequently reported in the literature in decibels relative to 1 angstrom or **1x10^{-10}** m.)

Very erroneous results are possible if equation 1.5 is applied inappropriately. This equation applies only to a very simple, uniformly radiating, pulsating sphere. This equation and others like it will, at best, provide only a rough guess of particle displacement given acoustic pressure for the vast majority of natural and man-made sound sources found in nature or commonly used in experimentation.